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Breeding Seasons and Annual Cycles of Trinidad Land-birds[1]

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(Text-figures 1-11)

[This paper is a contribution from the William Beebe Tropical Research Station of the New York Zoological Society at Simla, Arima Valley, Trinidad, West Indies. The Station was founded in 1950 by the Zoological Society's Department of Tropical Research, under Dr. Beebe's direction. It comprises 200 acres in the middle of the Northern Range, which includes large stretches of government forest reserves. The altitude of the research area is 500 to 1,800 feet, with an annual rainfall of more than 100 inches.

For further ecological details of meteorology and biotic zones see "Introduction to the Ecology of the Arima Valley, Trinidad, B.W.I.," by William Beebe, Zoologica, 1952, Vol. 37, No. 13, pp. 157-184].

Introduction

A survey of the breeding seasons of the land-birds was one of the principal investigations undertaken during 4½ years' residence at the New York Zoological Society's field station, now the William Beebe Tropical Research Station, situated in the Arima Valley in the center of the Northern Range of Trinidad (Text-fig. 1). This paper presents the results of the survey and attempts to relate the Trinidad breeding seasons to the general pattern of breeding in the northern part of South America.

The basic field work consisted of the finding and recording of nests and the systematic trapping and examining of as great a variety of species as possible in every month of the year. Those species that nest in traditional sites, or whose nests are abundant and easily found, could be investigated systematically and their breeding seasons accurately determined, but the nests of others are difficult to find and some were never found. Likewise, some species were trapped in large numbers, others in small numbers irregularly, and others not at all. Thus the information on the various species is necessarily of varying degrees of completeness. The biggest gap is the absence of any records for the diurnal birds of prey, which in some other parts of the tropics have been found to have somewhat different breeding seasons from most other land-birds (*e.g.*, Africa; Moreau, 1950).

A special effort was made to determine the breeding seasons of several forest species accurately, by regular searching along certain stretches of forest stream and trail in the Arima Valley. These "beats" were covered approximately weekly throughout the year, some for 4½ years and others for shorter periods. As a result, the breeding seasons of five species whose nests could be found in large numbers were determined with certainty, and even for species of which only 10 or 20 nests were found by this means the information so obtained is probably reliable.

For three years, a systematic weekly search was also made in a few acres of orchard at Arima, four miles from the main study area. Here, where there were only well-spaced small trees and bushes which could easily be inspected, a fairly complete account could be kept of the nesting of a limited number of typically savanna species.

As mentioned in the next section, a large number of nest records also came from the Sangre Grande area in eastern Trinidad, mainly from cultivated country with citrus, cocoa and small gardens. This area, some 15 miles east of the Arima Valley, has a less seasonal climate with a very high rainfall. Smaller numbers of records came from savanna country along the southern edge of the Northern Range, from the

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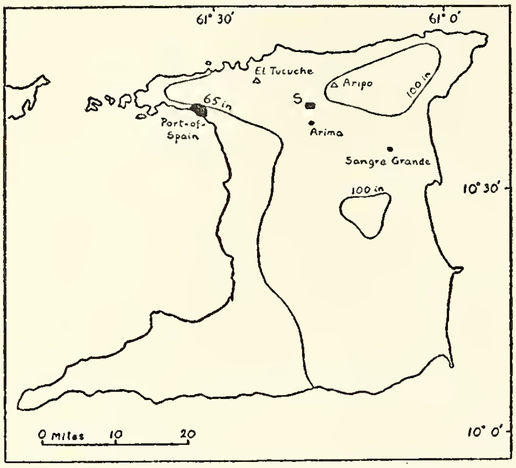


TEXT-FIG. 1. Map of Trinidad, showing 100-inch and 65-inch isohyets. S: the main study area, in the central part of the Arima Valley.

Port-of-Spain area in the northwest of the island, where the climate is drier than in the Arima Valley, and from various other localities, but none from the extreme south of the island. Thus there are records from forest, savanna, plantations and gardens, but the different areas of Trinidad are unequally represented.

In addition to the actual finding of nests, a small number of breeding records were based on the observation of recently fledged young birds. But except for a few specimens with full-sized eggs in the oviduct, gonad state was not used, although a considerable number of specimens was examined. For some species at least, fully developed testes in the male are not a good guide to the breeding season, since a state of full development is maintained for far longer than the female's egg-laying period.

The trapping and banding program provided important ancillary information on the season of moult. Indeed, as will become clear, in a study which is essentially concerned not only with the breeding season but with the whole annual cycle, knowledge of the season of moult is perhaps even more important than knowledge of the breeding season, as it seems to be the less variable of the two and may be more directly connected with the timing of the annual cycle.

Systematic recording of song-periods gave further information on the annual cycle. Weekly notes were made on the songs of 39 species, most of them for a period of three years or more. For many of them, the song period was found to coincide closely with the breeding season (as Skutch (1950) has also found for Central America), so that for those whose breeding season is not well known the evidence from the song period may be a useful guide as to its probable extent.

Acknowledgments

By great good fortune, shortly before this investigation began, the Trinidad Regional Virus Laboratory began a virological study of nestling birds which continued for over three years, from 1956 to 1959. In the course of this work one or two field assistants were employed throughout the year in systematic searching for nests in an area some 15 miles east of the Arima Valley. From April, 1957, one of us was associated with this work and an effort was made to improve and standardize the field assistants' recording methods. We are extremely grateful to Dr. W. G. Downs, former Director of the Trinidad Regional Virus Laboratory, for putting these records, amounting to over 900, at our disposal, and to him and Dr. T. H. G. Aitken for their help in the field in the course of this program.

Early in 1957, an attempt was made at a meeting of the Trinidad Field Naturalists' Club to introduce a nest record scheme for Trinidad, like those now operating successfully and on an increasing scale in several northern countries. The response was poor, and it became clear that there is as yet too small a number of people deeply enough interested in natural history for such a scheme to work, but three keen amateur ornithologists, Commander C. S. Bushe, Mr. R. P. ffrench and Mr. J. Dunston, maintained a continuous and valuable supply of nest records, and Dr. V. C. Quesnel supplied some old records. The record cards thus received totalled over 200 and formed a valuable addition to the collected data for which we are most grateful. We are also grateful for smaller numbers of unpublished records from Dr. William Beebe, Mr. W. Conway and Mr. C. T. Collins.

R. P. ffrench and C. T. Collins, working in the same areas as we worked and using the same methods, continued to trap and record moult in the year after our departure from Trinidad. Their data, which they have generously put at our disposal, add substantially to our own records.

Finally, we acknowledge with gratitude National Science Foundation Grants G 4385 and G 21007, without which this study could not have been carried out.

The Published Records

Williams (1922) gave precise and detailed records of the breeding of a limited number of species in Trinidad, based on residence over several years; these have been incorporated with our own data. Belcher & Smooker's series of papers (1934-37) provide a great deal of information on the breeding of Trinidad birds, which has recently been incorporated in a standard work (Herklots, 1961). Yet the information given in these papers is unsatisfactory in several ways. In the first place, for many species we have found that the breeding seasons given by Belcher & Smooker are far too short. Secondly, for most species they give a general statement, without specifying the number of records on which it is based. Thirdly, some of the nests were undoubtedly wrongly identified. Consequently, we have used their information only in cases where they clearly record all the nests found and there is no question of misidentification.

There have been a few other published records. Most concern species of which we have adequate records, and have not been used; but a small number refer to species whose breeding is little known (*e.g., Nyctibius griseus, Ramphastos vitellinus, Formicarius analis*), and these have been used. The source of all the records is given in the tabulated summary of breeding forming the Appendix to this paper.

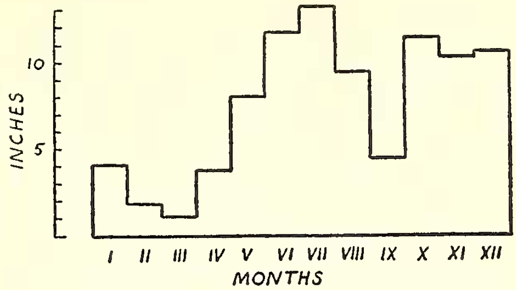
The Environment

Lying between latitudes 10° and 11° north, Trinidad has a generally humid climate and supports a natural vegetation which is almost entirely forest, ranging from rain-forest in the wetter parts of the lowlands and hills, through semi-seasonal and seasonal forests over the greater part of the lowlands, to strongly seasonal monsoon forest in the driest areas in the northwest (Beard, 1946).

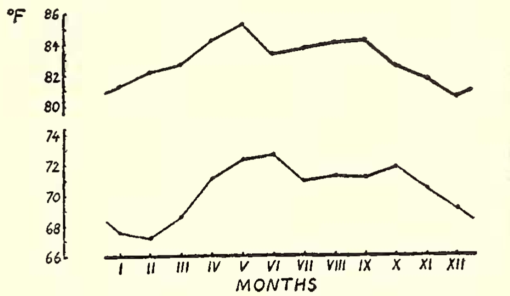
Physical Factors

As in most parts of the tropics, the seasons are determined mainly by the changing rainfall. There is a single long dry season, beginning in January and ending variably, usually in May, and a single wet season lasting for the rest of the year, which is often broken by a short dry spell (the "petit carême") in September or October (Text-fig. 2). During the dry season there is usually some sporadic rainfall, which may be heavy, in each month; precipitation averages an inch or two in February and March, the two driest months. In the wet season monthly averages of over 10 inches are common, except in the drier western parts of the island and on the coasts.

Mean temperature varies rather little, but is slightly lower from November to March than in the other months, and this is due especially to a decrease in the nightly minima. To this extent the "winter" is still felt only ten degrees from the Equator. The rise in mean minima from



TEXT-FIG. 2. Means monthly rainfall, Arima Valley, 1957-1959. (Text-fig. 10 shows the rainfall for the five years 1934-1938.)



TEXT-FIG. 3. Mean monthly maximum and minimum temperatures, St. Patrick's Estate, Arima Valley.

February to May constitutes the most striking temperature change of the year (Text-fig.3).

The trade winds blow persistently from the northeast during the dry season, and the weather then is at its pleasantest, especially in January and February when night temperatures regularly fall to the lower 60's F. (16-18°C.) In the wet season the wind tends to blow from the southeast and is more variable; nights are warmer and more humid, and day temperatures more variable than in the dry season because of the varying cloud cover. The rain usually falls in heavy downpours and wet spells rarely last for more than two days. At all seasons of the year there is much sunshine.

At 10° 40′ N., the latitude of the Arima Valley where most of the observations were made, day-length varies by only 75 minutes in the course of the year, the longest day being 37½ minutes more and the shortest 37½ minutes less than 12 hours. The fastest rate of change of day-length, at the time of the equinoxes, is a little under half a minute per day, while for a considerable period at the summer and winter solstices day-length is practically constant.

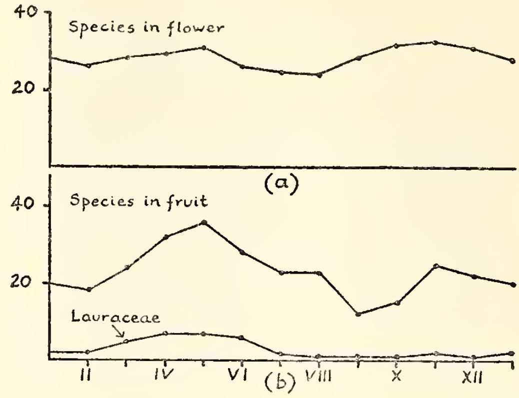
The Vegetation

As already mentioned, the wettest parts of Trinidad are in the northeast. Here the natural vegetation is evergreen forest. The driest part is the northwest corner. Here, at the extreme northwest point of Trinidad, and especially on the off-lying islands which reach out towards the Paria peninsula of Venezuela, a xerophytic and mainly deciduous vegetation prevails, in which cactuses are prominent. A distance of only 30 miles separates these extremes. The natural vegetation of the greater part of Trinidad, with annual rainfalls of 70-100 inches, is lowland forest which according to rainfall is more or less seasonal, *i.e.*, contains a more or less important deciduous element. There is also some natural savanna, edaphic in origin, lying mainly in a belt along the southern edge of the Northern Range, and some mangrove swamp and other forms of coastal vegetation.

It will be apparent that conditions in the Arima Valley, almost exactly in the middle of the Northern Range, must be intermediate between the wet and the dry extremes. In fact its climate is nearer the wet extreme, the annual rainfall averaging nearly 100 inches, and the natural vegetation of the lower part of the valley, the center of the study area, is transitional between lowland seasonal forest and lower montane rain forest, as defined by Beard (1946). Further details of the climate and vegetation of the Arima Valley are given in Beebe (1952) and Snow (1962a).

Especially in the western part of the island, much of the original forest has now been cleared, swamps have been drained and there is extensive cultivation of sugar, citrus fruits, cocoa, coconut and other tropical crops. But nearly 30% of the land surface of Trinidad is still under forest.

The changing seasons affect the appearance of the forest strikingly. Most of the trees have well-defined flowering and fruiting seasons, many have well-marked seasons of leaf fall and renewal of leaf, and all the individual trees of the same species are usually well synchronized in any given area. In general, there is most loss of leaf during the dry season, and most renewal of leaf in the wet season. Trees with conspicuous blossoms flower mainly at the end of the wet season and in the dry season (December-May), so that one's first impression is that this is the main flowering season. But many species are in flower in every month, and more systematic observation showed that in our area the number of tree species in flower was somewhat greater in May and October-December than in other months (Text-fig. 4a). For shrubs and herbs, the seasonal variation in flowering was rather similar, but many of them have much more protracted flowering seasons than the trees. However, it is important to note that many of the trees and shrubs that flower in the wet months have small, relatively inconspicuous flowers, and though these are exploited by the specialized nectar-eating birds, the supply of nectar is probably greatest in the dry season.



Text-fig. 4. Flowering and fruiting seasons in the Arima Valley. (a) number of tree species in flower in different months; (b) number of tree species in fruit; upper line, all species; lower line, Lauraceae.

Ripe fruits of many kinds are available throughout the year, but more different kinds ripen in the months April-June (the end of the dry and beginning of the wet season) than at any other time. There is also a second, minor peak of fruit abundance in November (Text-fig. 4b).

The rather ill-defined peaks of flowering (in May and November) coincide with the two much better defined but more unequal peaks of fruiting, and appear to some extent to be related to them. Thus many of the trees that contribute to the November peak of flowering ripen their fruit in the following dry season and so contribute to the April-June peak of fruiting, and similarly many of those that contribute to the May peak of flowering have ripe fruit at the end of the year and so contribute to the November peak of fruiting. But we made systematic observations on the fruiting seasons only of trees with fleshy fruits, eaten by birds, and the above generalizations may not apply, and indeed in individual cases do not apply, to trees producing other kinds of fruit.

Insect life is abundant at all times, but is probably at its height at the beginning of the wet season. It is then that mosquitoes and Lepidoptera breed most actively and termites swarm after heavy falls of rain. Then, too, the invertebrates of the forest floor become more accessible to ground-feeding birds as the earth, parched after weeks of dry weather, is again softened. Thus both for insectivorous and frugivorous birds food is probably at its most abundant in the early part of the wet season.

Breeding Seasons of the Land-birds

Presentation of the Results

As in most recent studies, the breeding date is taken to be the date on which the first egg was known or calculated to have been laid. For convenience, the data are grouped by months, in spite of the fact that all months are not of quite the same length. In the small proportion of cases where the calculated laying date falls within a period spanning two months, the middle date has been used.

The breeding and moult records for all species are tabulated in the Appendix, which is designed to be used as a general reference to the sections that follow. Fuller details are given in these sections of the breeding and moulting seasons of those species for which the information is especially complete.

Unless otherwise stated, "moult" and "moulting" refer to the complete moult, involving the flight- and tail-feathers as well as the body-feathers and coverts. In the majority of the birds dealt with here, as in north-temperate birds, there is an annual complete moult following immediately after the breeding season. Partial moults, involving only the body-feathers and wing- and tail-coverts, are in general more protracted and less regularly seasonal. In many of the species which we trapped in good numbers, it appeared to be the rule for juveniles to undergo a partial moult in the course of their first few months after leaving the nest, and for their next moult, which was complete, to be more or less synchronous with the adults' post-breeding moult.

The replacement of the flight-feathers spans practically the entire period required for the replacement of the whole plumage, and so is a convenient criterion for identifying a bird undergoing a complete moult. There are further reasons why it is the only safe criterion to use when examining unknown individuals under field conditions. Such replacement of the body-plumage as may continue for a time after the wing-moult is complete cannot, in many species, be distinguished from partial moult; and a certain number of body-feathers, and also tail-feathers, may be found growing at any time, presumably due to accidental loss.

Tinamou (Tinamidae)

The nine records for the single species, *Crypturellus soui,* are from nine different months. We have no record for May, undoubtedly a chance gap as Belcher & Smooker say that most eggs are laid in that month. Calling is heard throughout the year, but we do not know whether it is associated with breeding activities. The evidence suggests a more or less continuous breeding season, with no very marked peaks. We have no moult records.

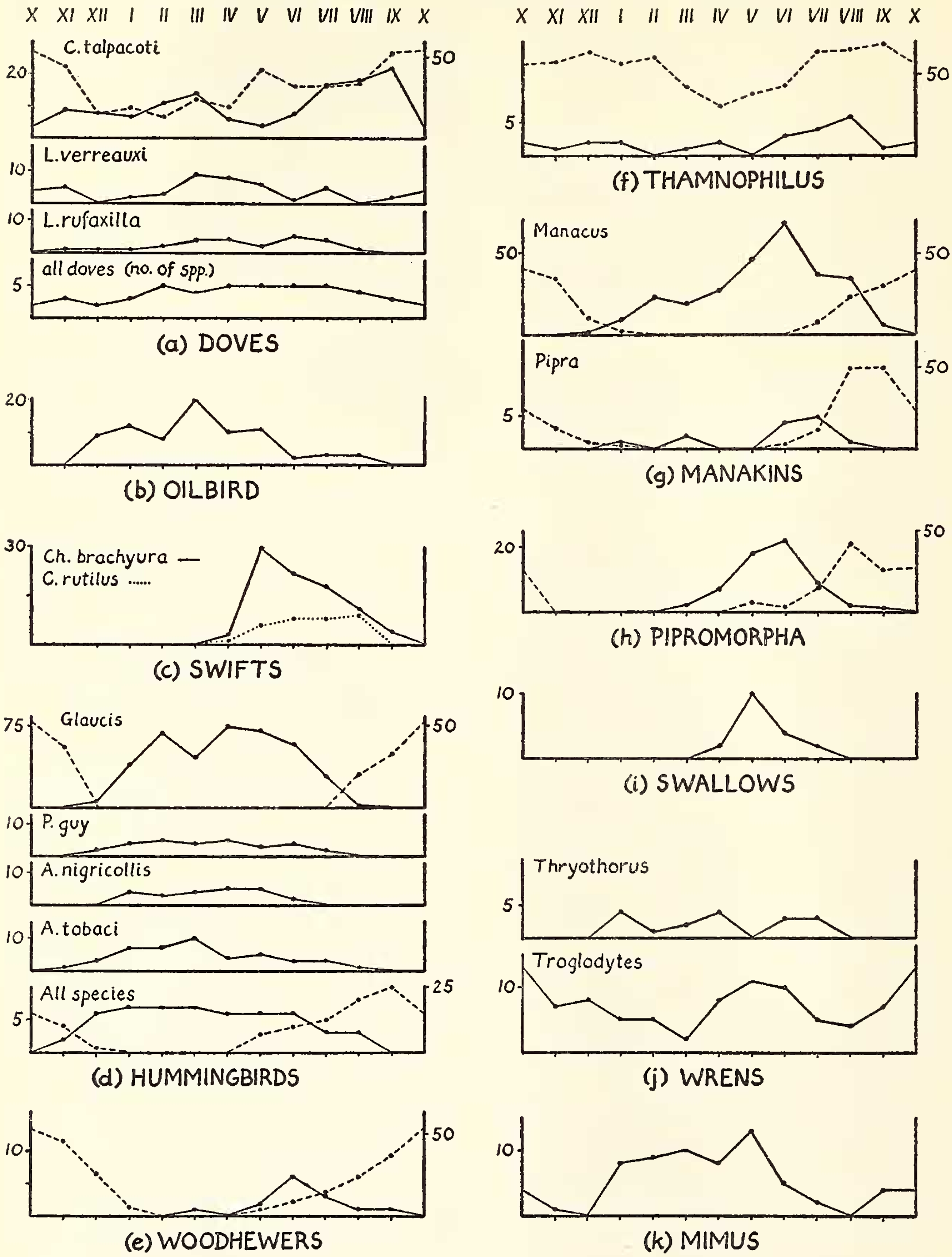
Pigeons and Doves (Columbidae)

A large number of records were obtained for *Columbigallina talpacoti,* and good numbers for *Leptotila rufaxilla* and *L. verreauxi.* All have very long breeding seasons (Tables I and II; Text-fig. 5a).

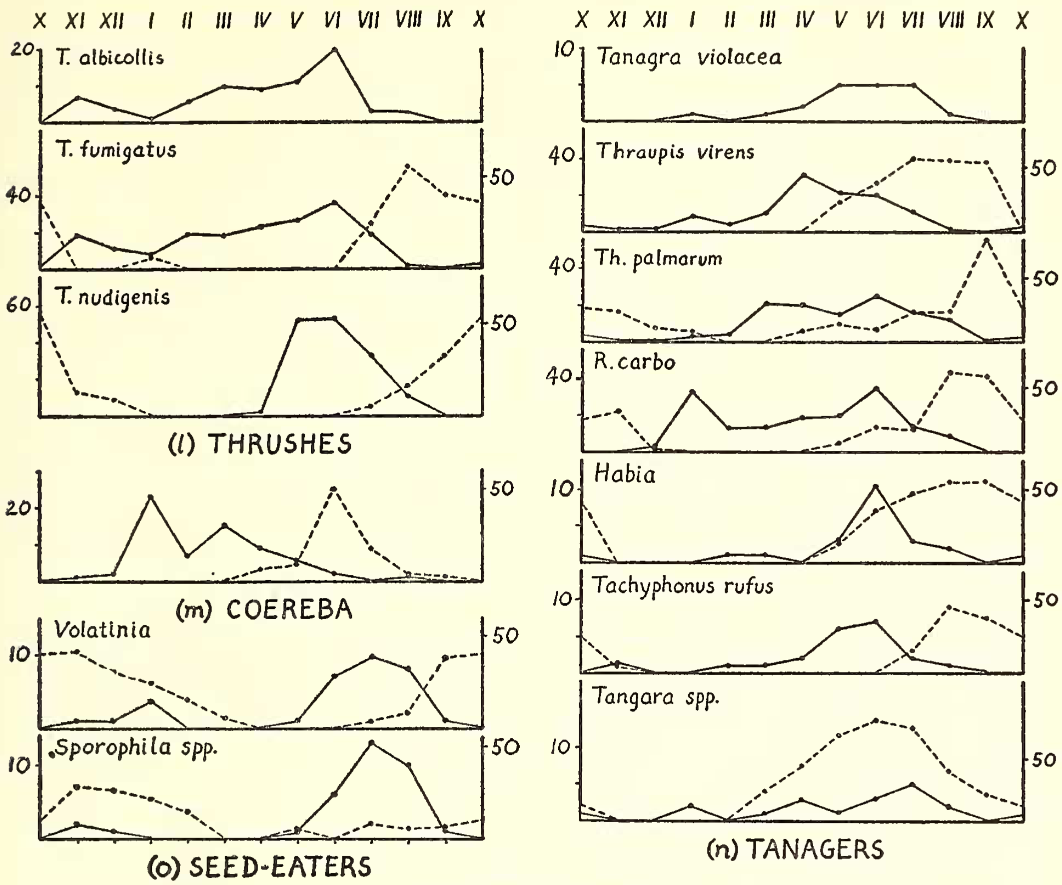
C. talpacoti was one of the few species found breeding in every month of the year. In an area of a few acres of orchard and garden at Arima which was searched systematically for three years, 60 nests were found, and 53 were found by less systematic searching by Trinidad Regional Virus Laboratory field assistants over 3½ years, near Sangre Grande 15 miles east of Arima (Table I). The Arima nests were grouped in two main periods, with greatest numbers in July-September and November-January and an almost complete gap in March-May (two nests only); and the pattern was similar in each year. The seasonal distribution of the Sangre Grande nests was rather different: they were recorded in every month except December, and 21% of them were in the months March-May.

The difference between the two sets of records may have been partly the result of different local climates. At Arima, with a fairly severe dry season, the nests were concentrated towards the ends of the two wettest periods of the year, perhaps in response to the ripening of the grass and weed seeds which probably form this dove's main food. At Sangre Grande, situated in the wettest part of the island, the climate may allow a more continuous production of suitable seeds. That the birds were indeed responding to favorable local conditions was suggested by the observations at Arima. Often, three or four nests would be started in a small area within a week or two of each other, after a period of inactivity.

The opportunist nature of the breeding of this species was also indicated by its moult. In the first place, unlike most other species which were examined, birds undergoing wing-moult were caught in nearly every month of the year (Table I). More notably, several of those that were not moulting showed evidence of "arrested" moult (Miller, 1961); that is, they had primary feathers of different ages in the wing, some of the outer ones being plainly older and more worn than the inner ones. In all of them, the moult had been arrested at a late stage, with two, three or four outer primaries still unshed. The most



TEXT-FIG. 5. Breeding and moulting seasons of different families and species. The number of nests is shown by a solid line, the scale being on the left-hand side, and the percentage of trapped birds in moult by a broken line, the scale being on the right-hand side. (The moulting percentage has been smoothed for *T. nudigenis, Volatinia, Thraupis virens, T. palmarum, Habia* and *Tachyphonus rufus.*)



TEXT-FIG. 5 *(Continued)*

reasonable explanation of this situation is that the birds had begun to moult and then stopped before the wing-moult was complete, presumably because local conditions had stimulated them to breed. Arrested moult has been described in other tropical species, *e.g., Pycnonotus xanthopygos* (Moreau *et al.,* 1947) and *Zonotrichia capensis* (Miller, 1961), and in the latter species it was proved to be connected with a resumption of breeding activities.

It is doubtful whether the figures justify drawing any distinction between the breeding season of *Leptotila verreauxi,* a dove of orchard and plantation, and *L. rufaxilla,* a forest dove. In both the period of greatest activity is March-July. These are also the months when the greatest number of different species of doves were found breeding (Table II).

Parrots (Psittacidae)

The four records for *Touit batavica* are all in the first three months of the year. We have no records for other species, but for *Forpus passerinus* Belcher & Smooker record egg-laying in April and May; and for *Amazona amazonica* the literature records are for March, April and May, and the local people agree that April is the month for collecting nestlings. For the family as a whole, January-May can thus be taken as the main laying period. We have no moult records.

Cuckoos (Cuculidae)

Adequate information was obtained only for *Crotophaga ani.* It was found breeding in every month, with no clear indication of any peak. In Cuba, *C. ani* breeds only in the wet season (Davis, 1940), and in Central America the very similar *C. sulcirostris* also breeds in the wet season (Skutch, 1959). The Trinidad nests, which were mainly found in the wetter eastern half of the island, do indeed show a slight tendency to be concentrated in the wet part of the year: 45 (68%) of them were in the six months following the onset of the rains (May-October); but there was only one in December, one of the wettest months, and eight in February, one of the driest months.

Little information was obtained on the moult.

TABLE I. BREEDING AND MOULTING OF *Columbigallina talpacoti*

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Breeding season at Arima	4	3	1	1	—	3	9	11	15	1	4	8
Breeding season in Sangre Grande area	2	6	12	4	3	4	4	5	6	3	4	—
Number in moult in each month, as a fraction of total trapped	2/44	10/38	0/2	0/0	1/2	2/5	1/5	3/8	1/1	2/2	2/6	7/17

NOTES, applying also to Tables II-XIII. The breeding season is shown by the number of nests in which the first egg was laid in the month indicated. The moulting season is shown by the number of individuals trapped which were undergoing wing-moult in the month indicated, as a fraction of the total number trapped in that month.

Nine of the 17 adults examined were moulting their flight-feathers in the months March, June, July, August and November. The sequence of replacement of the wing-feathers is highly irregular, as in some other tropical cuckoos (Stresemann & Stresemann, 1961). Here again there is evidence of emancipation from a fixed annual cycle.

Owls (Strigidae and Tytonidae)

All the nine records for *Otus choliba,* and five of the six for *Glaucidium brasilianum,* are in the months February-May. The literature records for the three other species are also nearly all in the same months: *Ciccaba virgata,* April (2) (Belcher & Smooker); *Pulsatrix perspicillata,* January, March (2) (Cherrie, 1908; Belcher & Smooker); *Tyto alba,* February (2), April, May (Belcher & Smooker). We have no moult records.

Oilbird (Steatornithidae)

The breeding season of *Steatornis* has been dealt with fully in an earlier paper (Snow, 1962 (1963) d). Clutches were laid in every month except October and November, most being from December to May (Text-fig. 5b). Most young are in the nest from April to June, and it was found that this is also the period when the greatest number of the Oilbird's food trees have ripe fruit (Text-fig. 4b). The relationship between breeding and moulting was not clear. Both the breeding cycle, from egg-laying to the fledging of the young, and the moult are very long processes, lasting several months. Most moulting takes place in the months June-November, when there is least egg-laying, but the year is not long enough to accommodate separately the time taken in breeding activities and that needed for the moult, and it seems that the processes of breeding and moulting must frequently overlap.

Nightjars (Caprimulgidae)

Uncertainty of identification makes some of the literature records doubtful, but the bulk of all records are in the months March-May, the full extent being from January to August. We have no moult records.

Potoo (Nyctibiidae)

Five of the six records are in March and April, and the sixth in July. We have no moult records.

Swifts (Apodidae)

The swifts have been dealt with fully in an earlier paper (Snow, 1962b). The two species for which there are adequate records *(Chaetura brachyura* and *Cypseloides rutilus)* breed in the early part of the wet season, from late April or May to late August or September (Text-fig. 5c). Thus their young are in the nest at the time when flying insects are probably at their most abundant. The moult follows close after breeding, birds undergoing wing-moult being nearly all caught in the months August-November.

The suggested adaptive relationship between the swifts' breeding season and the abundance of their food supply is supported by the more limited data for the swallows (p. 12), which exploit a similar food supply—small flying in-

TABLE II. BREEDING SEASONS OF *Leptotila rufaxilla* AND *L. verreauxi*

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Leptotila rufaxilla	1	1	4	4	2	5	3	—	—	—	1	1
Leptotila verreauxi	2	3	9	8	6	1	5	—	2	4	4	—
Number of dove species breeding in each month	3	4	4	5	4	5	5	2	3	2	3	2

sects—and have rather similar breeding seasons. The earlier breeding seasons of the nightjars and potoo, which also take flying insects, may be related to their more exposed nest-sites, favoring breeding in the dry season, or it may be that the larger crepuscular and nocturnal insects on which they feed are more active or more easily visible at this season.

Hummingbirds (Trochilidae)

There is information for eight species, including very full records for *Glaucis hirsuta* and less numerous but adequate records for *Phaethornis guy, Anthracothorax nigricollis, Amazilia tobaci* and *Chrysolampis mosquitus*. The season is a long one, beginning at the end of the year (November in two species, December in three species) and continuing to July or August. All the species for which the data are adequate show approximately the same extent of breeding. The moult takes place mainly from July to November, but a little from May onwards (Text-fig. 5d, Table III).

There was some evidence that breeding is a little later in forest than open country. Thus, in four years, *Glaucis* began in late December and January in open places, and a month or more later in closed forest. The nests of *Amazilia tobaci* in forest in the Arima Valley were all in the months February-July, those in open places from December onwards. The most strictly forest species of all, *Chlorestes notatus*, seemed to be especially late. All our records were in May and June, though Belcher & Smooker give a doubtful record of a March nest and we have seen birds collecting nest-material in late December and February.

In the four species for which records were kept over a period of four years, regular song was recorded throughout the year except for the time of moult, when it was either much reduced *(Amazilia tobaci)* or ceased entirely for several weeks *(Amazilia chionopectus, Phaethornis guy, P. longuemareus)*.

The hummingbird breeding season covers the whole of the dry season, with a little breeding starting well before, when the weather is still very wet, and a good deal of breeding continuing for about two months after the wet season has begun. Thus there is no very exact correlation between hummingbird breeding seasons and weather. It has already been mentioned that the number of species of trees and other plants in flower is high in all months of the year, but that in general the trees with large and conspicuous blossoms, which are especially attractive to hummingbirds, flower mainly from December to May, while those that flower in the wet season mainly have smaller flowers which probably provide less nectar. Similarly the most important of the herbs and vines which are exploited by hummingbirds flower mainly in the dry season (especially *Heliconia* spp., *Justicia, Norantea, Pachystachys)*. Thus the main part of their breeding season in Trinidad probably coincides with the period of greatest availability of nectar, but here again, due to the length of the breeding season, synchronization cannot be exact. It is significant that, among the other birds for which there is information, the breeding season of *Coereba flaveola*, the most pronounced nectar-feeder, is most like that of the hummingbirds (p. 14).

Kingfishers (Alcedinidae)

We had no breeding records; those given by Belcher & Smooker for three species of *Chloroceryle* are all in the months March-September. Two individuals of *C. americana* were trapped twice. One was moulting in September (moult well advanced) and not in the following July; the other was moulting in November (moult

TABLE III. ANNUAL CYCLES OF EIGHT SPECIES OF HUMMINGBIRDS

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Breeding season of:												
Glaucis hirsuta	38	69	46	75	71	58	28	1	—	—	—	6
Phaethornis guy	4	5	4	5	3	4	2	—	—	—	1	2
Phaethornis longuemareus	4	5	2	—	—	1	—	—	—	—	—	1
Anthracothorax nigricollis	4	3	4	5	5	2	—	—	—	—	—	—
Chrysolampis mosquitus	5	6	5	4	9	—	—	1	—	—	—	1
Chlorestes notatus	—	—	1	—	2	2	—	—	—	—	—	—
Amazilia chionopectus	1	3	2	1	1	—	—	—	—	—	—	1
Amazilia tobaci	7	7	10	4	5	3	3	1	—	—	1	3
Number of species breeding in each month	7	7	8	6	7	6	3	3	—	—	2	6
Number of species moulting in each month	—	—	—	—	1	1	4	5	6	5	4	1

nearly completed) and not in the following February. Six other individuals trapped in December, April, May and June were not moulting. These records, though few, suggest that August-November are the usual months of moult.

Trogons (Trogonidae)

The six breeding records available are well distributed throughout the year, with the suggestion of some concentration in the months February-May. One bird trapped in July was moulting; six others, trapped in March, June, July and October were not. Calling was recorded throughout the year. The evidence points to a long and perhaps ill-defined breeding season, but is too scanty for any firm conclusion.

Motmot (Momotidae)

All seven breeding records for the single species, *Momotus momota*, are in April and May. The moult records are in June, July and October. The moult must take a long time for each individual, as a bird which was in an early stage of wing-moult on June 26 (8 old primaries remaining) was still moulting on October 1 (2 old primaries remaining).

Jacamar (Galbulidae)

All except one of the 17 records for the single species, *Galbula ruficauda*, are in the months February-April, the exception being in June. We have only a single moult record, also in June.

Toucan (Ramphastidae)

The four records, all from the literature, for the single species, *Ramphastos vitellinus*, are from March to June (Belcher & Smooker; Chenery, 1956). We have no moult records.

Woodpeckers (Picidae)

The best information is for *Celeus elegans* and *Piculus rubiginosus*. Breeding records are in the months April-May and March-May respectively, and moult records in July-November and August-September respectively. In *Celeus* the moult must take well over four months for the individual, as one bird trapped twice while moulting had replaced only four of the ten primaries in nine weeks. *Veniliornis kirkii* appears, from the few records, to breed a little earlier than these two. Belcher & Smooker's records for *Ceophloeus lineatus* and *Phloeceastes melanoleucus* suggest breeding seasons similar to those of *Celeus* and *Piculus*.

Woodhewers (Dendrocolaptidae)

Few breeding records were obtained for the two common species, *Xiphorhynchus guttatus* and *Dendrocincla fuliginosa*, but combined with the moult records and their periods of calling they gave a reasonable picture of the annual cycle (Table IV, Text-fig. 5e). Both species breed mainly in the first half of the wet season (May-July), and moult in the second half of the year. The full extent of the breeding season appears to be from March to September, the records for *Xiphorhynchus* being on average earlier than those for *Dendrocincla*. Both species begin to call soon after the beginning of the year and continue until early October, with *Xiphorhynchus* again starting rather earlier than *Dendrocincla* (usually mid-January and mid-February respectively).

Spinetails (Furnariidae)

The four species for which there are records are ecologically very different from each other. *Sclerurus albigularis*, a ground-living forest bird and a tunnel-nester, has a breeding season which is apparently confined to the "winter," having its peak in December-January, a season unmatched by any other Trinidad bird. *Synallaxis albescens*, a species of semi-open country, has an extended breeding season, the 17 records being from eight different months, and that of *S. cinnamomea*, a forest species, appears also to be extended. *Certhiaxis cinnamomea*, a swamp bird, breeds from June to October, a restricted and late breeding season similar to

Table IV. Annual Cycles of Two Species of Woodhewers

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Dendrocincla fuliginosa												
Breeding season	—	—	—	—	2	4	1	1	1	—	—	—
Number in moult in each month, as a fraction of the total trapped	0/7	0/6	0/7	0/6	0/4	1/12	0/14	2/9	2/4	0/1	4/6	1/2
Xiphorhynchus guttatus												
Breeding season	—	—	1	—	—	2	2	—	—	—	—	—
Number in moult in each month, as a fraction of the total trapped	0/2	0/1	0/2	0/2	0/0	1/2	1/1	1/3	2/2	0/0	0/2	0/0

that of other passerine birds confined to swamps (*Fluvicola, Arundinicola, Agelaius;* see later).

Moult data were obtained only for *Certhiaxis,* in which two out of the three birds trapped in both November and February were undergoing wing-moult.

Antbirds (Formicariidae)

Antbird nests are notoriously difficult to find, and disappointingly few records were obtained for this family. Only for *Thamnophilus doliatus* do the records form a satisfactory basis for discussion. This species has an extended breeding season, with nests recorded in ten of the twelve months (Table V, Text-fig. 5f). It was also found to moult in almost every month of the year. The percentage of trapped birds undergoing moult was unusually high, and irregularities in the sequence of the wing-moult were far commoner than is usual in passerine birds. *Thamnophilus* lives in pairs throughout the year, calling is heard in all months, and it is difficult to avoid the conclusion that the species as a whole has no well-defined annual cycle (though individual pairs may show annual periodicity). Observations in Tobago (25 miles northeast of Trinidad) suggested that there may be local outbursts of breeding, stimulated by favorable conditions. Thus in July, 1961, during rather wet weather, four occupied nests were found in a limited area where none had been found on previous visits.

Taraba major, Formicarius analis and *Myrmeciza longipes* were also found to call throughout the year, with no marked fluctuations in intensity, and less complete records suggested the same for *Dysithamnus mentalis.* The few records for species other than *Thamnophilus* suggest that breeding may be at its height in the months May-August, but are quite inadequate for further discussion.

Cotingas (Cotingidae)

Too few breeding records are available for *Pachyrhamphus, Attila* or *Tityra* to permit generalizations. Six breeding records of *Procnias averano* were obtained in the course of a detailed study of this species to be published elsewhere (B. K. Snow, in preparation), and there is one dated literature record (Beebe, 1954). These records, and field observations of display and copulation, indicate that the breeding season is in two parts, with a short laying period in late October and November and a more extended laying period in the months April-August. The moult is at its height in September. The moulting season of the other species is not known, but the otherwise more or less continuous calling of *Attila* is considerably reduced in the months July-September, which suggests that for it, too, this is the time of moult.

Manakins (Pipridae)

The breeding seasons of the two species of manakins have been dealt with in earlier papers (Snow, 1962a and 1962 (1963) c). The data are very full for *Manacus manacus;* for *Pipra erythrocephala* the information is less good, but its breeding season seems to be essentially the same. The full extent of the breeding season is from early January, or exceptionally the end of December, to early September, but breeding activity is variable and not usually intense in the first three months of the year, and it does not reach its peak until April-June. Both species moult at the same season, mainly from August to November (Table VI, Text-fig. 5g). It was shown in the earlier papers that more kinds of fruits suitable for manakins are available in the months April-June than at any other time of year (see also Text-fig. 4b), and as insects are probably also at their most abundant at this time it was concluded that there were strong grounds for postulating an adaptive relationship between the breeding season and the seasonal fluctuations in food supply. In *Manacus,* there were annual differences of several weeks in the time of the start of breeding, the significance of which is discussed later (p. 18).

Flycatchers (Tyrannidae)

The flycatchers are an ecologically very diverse group of predominantly insectivorous birds. The 18 species for which data were obtained can be divided fairly satisfactorily into four groups by habitat: birds of forest, open woodland and plantation, savanna, and swamp. The six forest species have, as a group, a well-defined breeding season from March to September (Table VII). This is also the extent of the

Table V. Breeding and Moulting of *Thamnophilus doliatus*

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Breeding season	3	3	—	1	2	3	2	—	2	1	1	1
Number in moult in each month, as a fraction of the total trapped	2/2	0/1	1/2	2/4	0/4	3/5	4/7	6/8	1/2	2/3	1/2	2/4

TABLE VI. ANNUAL CYCLES OF *Manacus manacus* AND *Pipra erythrocephala*

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Manacus manacus												
Breeding season	9	23	19	27	46	69	37	35	6	—	—	1
Number in moult in each month, as a fraction of the total trapped	1/46	0/23	0/22	0/38	0/49	1/111	6/76	23/88	18/60	13/32	18/56	5/47
Pipra erythrocephala												
Breeding season	1	—	2	—	—	4	5	1	—	—	—	—
Number in moult in each month, as a fraction of the total trapped	0/74	0/34	1/46	0/30	0/36	1/72	8/64	52/104	46/92	14/58	10/84	3/78

breeding season of the single species for which a large number of records were obtained, *Pipromorpha oleaginea* (Table VIII, Text-fig. 5h). The seven species characteristic of open woodland and plantation have a longer breeding season, December and January being the only months in which no records were obtained, with a poorly marked peak in March-July; while the four savanna species were found breeding throughout the year, except for September. The ecological distinctiveness of the species placed in these two latter groups is less clear than between the other groups, and the habitats themselves intergrade.

There are only two species in the last group, and they appear to have a well-defined breeding season which is later than that of the forest group, being at its height from June to October. In this they agree with the other land-birds inhabiting swamps, and there is an obvious adaptive basis for their late breeding season. The swamps largely dry out during the dry season and flood again in the course of the wet season. The main annual increase in the invertebrate fauna probably coincides with the first months of rising water-level.

Swallows (Hirundinidae)

The 14 breeding records for *Progne chalybea* are all in the months April-July, and the four for *Stelgidopteryx ruficollis* all in April and May (Text-fig.5i). Doubtless the latter do not show the full extent of the breeding season. The only two *Stelgidopteryx* in moult, out of 14 trapped in four different months, were both trapped in August. From these records it is reasonable to conclude that the breeding season of *Progne*, and probably also *Stelgidopteryx*, is similar to, but perhaps a little earlier than, that of the swifts, and the same adaptive relationship with the food supply may be suggested.

Wrens (Troglodytidae)

Both species have long breeding seasons. *Troglodytes musculus*, a species associated with man and frequently nesting in houses, was found breeding in all months, with peaks in May and October (Text-fig. 5j), and *Thryothorus rutilus*, a forest species, from January to July, with a gap in May which is probably not significant.

A complete series of records kept for two or three pairs of *Troglodytes*, nesting in two houses in the Arima Valley over a period of 4½ years, showed less continuous breeding activity than is indicated by the combined records from all localities (Table IX). There was a marked peak in April-June, a complete gap in July-August, and a second more extended period of laying

TABLE VII. BREEDING SEASONS OF FLYCATCHERS

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
5 forest species	—	—	2	2	3	4	3	1	1	—	—	—
7 open woodland species	—	2	3	3	3	3	4	2	1	1	2	—
4 savanna species	2	4	4	4	4	4	3	2	—	1	2	2
2 swamp species	—	—	1	—	—	1	2	2	2	2	—	—

NOTE: Forest species: *Empidonax euleri, Platyrinchus mystaceus, Tolmomyias sulphurescens, Leptopogon superciliaris, Pipromorpha oleaginea.* Open woodland species: *Myiodynastes maculatus, Megarynchus pitangua, Contopus cinereus, Myiophobus fasciatus, Tolmomyias flaviventris, Myiopagis gaimardii, Camptostoma obsoletum.* Savanna species: *Tyrannus melancholicus, Legatus leucophaius, Pitangus sulphuratus, Elaenia flavogaster.* Swamp species: *Fluvicola pica, Arundinicola leucocephala.*

TABLE VIII. BREEDING AND MOULTING OF *Pipromorpha oleaginea*

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Breeding season	—	—	2	7	18	22	9	2	1	—	—	—
Number in moult, as a fraction of the total trapped	0/26	0/22	0/16	0/44	1/13	1/33	2/13	6/14	5/19	5/18	0/21	0/31

from September to January, followed by a nearly complete gap in February and March, the height of the dry season. The remainder of the records were nearly all collected by Trinidad Regional Virus Laboratory field assistants in the wetter Sangre Grande area, some 15 miles to the east. They are the only records that there was reason to suppose were biassed, since at times of the year when few other nests could be found (mainly in the months August-December), they concentrated on *Troglodytes*. But the records are interesting in showing that breeding is continuous, even though in this area too an unbiased sample might show peaks at the same time as in the Arima Valley.

Out of 24 *Troglodytes*, trapped in ten different months, and 25 *Thryothorus*, trapped in nine different months, only three birds were in moult, one *Troglodytes* in August and two *Thryothorus* in March and August. Both species sing throughout the year, but a marked resurgence of song was noted in *Troglodytes* in September. This is in accord with the July-August gap in breeding and the single moult record, and suggests that July and August are the main months of moult.

Mockingbird (Mimidae)

A fairly complete series of 41 records was obtained for three or four pairs of *Mimus gilvus*, the only representative of the family, nesting in gardens and orchards near the town of Arima over three years, and smaller numbers from other scattered localities (the species does not breed up the Arima Valley). The Arima records show a main period of breeding from January to July, with 88% of the nests in these months, and a minor period from September to November. The records from other localities also fall into these two periods in similar proportions (Text-fig. 5k). Though mockingbirds were not trapped, a break in July and August in the otherwise more or less continuous song-period, followed by a sudden revival of song in September, shows that the months July and August are almost certainly the height of the moult season, as in many other species. The double breeding season, with a minor peak following the moult and a major peak several months later, is essentially similar to the situation in *Troglodytes* in the Arima Valley, *Turdus albicollis* and *T. fumigatus* (below), *Thraupis palmarum* (p. 15), and perhaps other species, and is discussed in a later section (p. 23).

Thrushes (Turdidae)

The breeding seasons of the three *Turdus* species have been dealt with in detail in a previous paper (Snow & Snow, 1963). *T. fumigatus* and *T. albicollis* have very long breeding seasons, from later October or November to July or August, both with a minor peak in November and a major peak in June (Table X, Text-fig. 5l). The breeding season of *T. nudigenis* is much shorter, lasting from late April to August. Extensive trapping data for *T. fumigatus* and *T. nudigenis* showed that both moult at about the same time, the former in July-October and the latter in August-November. The song periods of all three species are co-extensive with their breeding seasons. The only plausible reason that suggests itself for the great difference between the breeding season of *T. nudigenis* and the other two species lies in their different habitat-preferences. *T. nudigenis* is a bird of semi-open country, where the effect of the dry season is more severely felt than in the forest, and the food supply for the young may be abundant enough only in the early part of the wet season. The other two are forest species, and so probably have a food supply that is less affected by the changing seasons. It may be noted that the two peaks in their long breeding season resemble those of *Mimus gilvus*, discussed above, and other species with very long breeding seasons.

Gnatcatchers (Polioptilidae)

Breeding records for the single species, *Ram-*

TABLE IX. BREEDING SEASON OF *Troglodytes musculus*

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Lower Arima Valley	4	1	—	3	6	4	—	—	2	5	4	2
All localities	5	5	2	8	11	10	5	4	7	13	7	8

Table X. Annual Cycles of *Turdus* species

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Turdus albicollis												
Breeding season	1	6	10	9	11	20	3	3	—	—	7	4
Turdus fumigatus												
Breeding season	8	19	18	23	26	36	19	1	—	2	18	11
Number moulting, as a fraction of the total	1/15	0/8	0/5	0/4	0/11	0/16	2/8	4/7	2/5	3/8	0/8	0/11
Turdus nudigenis												
Breeding season	—	—	—	2	52	53	33	11	—	—	—	—
Number moulting, as a fraction of the total	0/6	0/3	0/7	0/9	0/7	0/10	0/13	2/13	3/3	1/2	3/8	0/21

phocaenus melanurus, of doubtful affinities but provisionally included in this family, are from February to August, and there is a single moult record in December. The information is too slender for generalizations.

Vireos (Vireonidae)

Records are few, especially for *Hylophilus.* The five records for *Vireo olivaceus* are restricted to April, May and June, but agree well with the restricted period of calling (usually early March to July), so are probably a satisfactory indication of the breeding season. There is a single moult record for early August. (The species appears to be a migrant to Trinidad, since we had no records of its occurrence from October to mid-February). *Cyclarhis gujanensis* apparently breeds rather late, as all our five records were from June to November, but our moult records were in the same period and more are needed to clarify its annual cycle.

Honeycreepers (Coerebidae)

Coereba flaveola, the bananaquit, is included in this section for convenience, although it is probably closer to the New World warblers (Parulidae) than to the rest of the honeycreepers. It is a much more specialized nectar feeder than the others. The large numbers of breeding and moult records for *Coereba* show that the total extent of its breeding season is long, from November to June (with a single August record), but that most breeding takes place from January to May (Table XI, Text-fig. 5m). This is a season very similar to that of the hummingbirds, the only other primarily nectarivorous birds, and the same adaptive relationship may be suggested. Also as in the hummingbirds, the moult takes place from May to October.

Rather few records were obtained for the four typical honeycreepers *(Chlorophanes, Dacnis* and *Cyanerpes* spp.), but they agree in showing a later breeding season, from March to July, and a mainly later season of moult, August-November. These species depend far less on nectar than does *Coereba;* correspondingly, their breeding seasons show a peak which coincides with that of the bulk of other land birds. Only two records were obtained for the rather distinct *Conirostrum bicolor,* a mangrove bird, and no generalizations can be based on them.

Warblers (Parulidae)

Again, records are few. *Basileuterus* certainly breeds mainly in the first half of the year, as our five records are from March to June and the main period of song is from late December to June. For *Geothlypis,* a swamp bird, information is scanty, but since three of the four very scattered records are from May to October and it sings more in the wet season than in the dry, it may have a mainly late breeding season like the other swamp passerines. We have no records for *Parula pitiayumi,* which sings throughout the year, but Belcher & Smooker give two, in June and July. We have no moult records for these three species.

Table XI. Breeding and Moulting of *Coereba flaveola*

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Breeding season	23	7	15	9	6	2	—	1	—	—	1	2
Number in moult, as a fraction of the total trapped	0/28	0/16	0/10	0/43	1/14	2/21	5/10	7/40	2/63	1/38	0/33	0/41

Orioles and Allies (Icteridae)

The high, hanging nests of the large oropendola, *Psarocolius decumanus,* were never reached, but from our own observations and those of others (Tashian, 1957; Drury, 1962) January-May can safely be taken to be the breeding season. The smaller cacique, *Cacicus cela,* breeds at the same period, while *Icterus nigrogularis* has a longer and slightly later season. All these species build elaborate hanging nests in exposed positions. Nest-building is probably hindered by rain and the safety of the nests, once built, is probably endangered by very wet weather, so that the rather exact synchronization of breeding with the dry season seems to have a clear adaptive basis.

The breeding season of *Quiscalus lugubris* is divided into two parts, with a major period in May-August and a minor period in November-February. A fairly complete series of 19 records from a limited area at Arima, collected over a period of three years, and 12 scattered records from other localities, both fall into these two divisions. *Agelaius icterocephalus,* a swamp species, has a late breeding season, from June to November, similar to that of the other swamp birds already mentioned.

Of the two parasitic species, one, *Psomocolax,* breeds at the same time as its hosts, *Psarocolius* and *Cacicus;* the other, *Molothrus,* which parasitizes a large number of diverse species, breeds from April to October.

We have few records of moult, except for *Agelaius.* Out of 43 *Agelaius* trapped in mid and late January, 23 were moulting, nearly all of them being in a very late stage of moult, and the rest were in fresh plumage. Only one out of 16 trapped in June and July was moulting, and this appeared to be a young bird undergoing a moult involving some inner secondaries only. Thus it appears that its moult season, like its breeding season, is late.

Tanagers (Thraupidae)

Large numbers of records were obtained for *Ramphocelus carbo, Thraupis palmarum* and *T. virens,* and adequate numbers for *Tachyphonus rufus, Habia rubica* and *Tanagra violacea.* Moult data were also obtained for all these species; so that for these six we can be sure that the picture of the breeding season and annual cycle presented here is substantially correct (Text-fig. 5n). For the remaining species the information is rather scanty, except that the trapping records of *Tangara gyrola* and *T. mexicana* were numerous enough to show their season of moult. The two breeding records for *Piranga flava* are chiefly of interest as representing an addition to the known breeding birds of Trinidad.

Ramphocelus carbo has a long breeding season with two well-marked peaks, in January and June. In each year, in the Sangre Grande area where most of the records were obtained, a burst of nesting began in early January, with sometimes one or two early nests at the end of December. Breeding then declined in February and March, then rose to its second peak. Late nests occurred until August, with one in September. Birds were trapped in moult over a long period (May-December), but 80% of them in the months July-October (Table XII).

The two *Thraupis* species also have long breeding seasons. Nests of *T. palmarum* were recorded in every month and nests of *T. virens* in eleven months of the year. But both show a well-marked and rather similar seasonal pattern, with a major peak (apparently double in *T. palmarum*) from March to July or August, and a small peak in October in the middle of a five-month period (August-December) when relatively few nests are started.

For 4½ years, a complete record was kept of the nesting of *T. palmarum* in the crowns of three ornamental palms at Simla, in the Arima Valley. The 35 nests thus recorded show almost exactly the same seasonal distribution as the combined records from all localities; 29 of them (83%) were in the months March-July. They are further discussed on p. 23.

Moulting individuals of *T. virens* were trapped in the three months June-August, and the moulting *T. palmarum* over a longer period, from May to December (Table XII). The difference would probably be reduced by further records, but is probably genuine and related to the difference in the extent of their breeding seasons,

The three species for which less abundant data were obtained, *Tachyphonus rufus, Habia rubica* and *Tanagra violacea,* all have broadly similar breeding seasons, with a peak in May-June (sharper in some than others), little breeding in the four preceding months, and little or none from September to the end of the year. In all three, moulting birds were caught only in the months June-October.

The annual cycles of the *Tangara* species do not conform to the pattern which, with wide variations, is nevertheless general to the preceding six species. The few breeding records would not of themselves suffice to indicate anything unusual—nests in all months except February, September, November and December (months in which breeding activity is reduced in the other species); but the moulting regime is anomalous. In the first place, the season of moult is very early, beginning in April and being at its height

Table XII. Annual Cycles of Tanagers

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Thraupis palmarum												
Breeding season	3	4	21	20	15	25	16	12	1	3	1	1
Number in moult, as a fraction of the total trapped	0/3	0/2	0/3	0/1	1/7	1/5	0/8	3/4	0/0	2/2	1/8	1/6
Thraupis virens												
Breeding season	8	4	10	31	21	20	11	1	—	3	1	1
Number in moult, as a fraction of the total trapped	0/2	0/0	0/6	0/4	0/2	2/6	3/5	7/9	0/3	0/0	0/5	0/3
Ramphocelus carbo												
Breeding season	33	14	14	19	20	35	14	9	1	—	—	3
Number in moult, as a fraction of the total trapped	0/25	0/8	0/12	0/17	2/28	5/24	6/32	23/35	16/26	4/15	4/12	1/36
Tachyphonus rufus												
Breeding season	—	1	1	2	6	7	2	1	—	—	1	—
Number in moult, as a fraction of the total trapped	0/9	0/2	0/2	0/10	0/10	0/8	0/3	3/6	4/4	1/8	0/4	0/8
Number of tanager species breeding in each month	6	5	7	8	8	8	9	8	2	5	3	3
Number of species in moult in each month	—	—	—	2	3	6	4	9	6	4	3	2

from May to July, at the same time as the breeding season appears to be at its height (Text-fig. 5n). Furthermore, the individual moult seemed to be a much slower process in *Tangara* than in the other tanagers studied, and in *T. gyrola* there was evidence of "arrested" moult, as was also found in *Columbigallina talpacoti*. These points are discussed in more detail in a later section (p. 22).

Swallow-tanager (Tersinidae)

Belcher & Smooker give a June record for the single species, *Tersina viridis*. We have seen two pairs entering and leaving nest-holes in May, as though nesting or preparing to nest. The species appears to be migratory, as it is in northern Venezuela (Schaefer, 1953), since all except one of the records of its occurrence known to us are in the months March-June. We have no moult records.

Finches and Seed-eaters
(Fringillidae and Emberizidae)

As a group, the small finches and seed-eaters breed mainly later than most other land-birds with the exception of the swamp species. Of the 80 nests recorded, 64 were in the months May-September, and the remaining 16 all in the following four months. (Table XIII, Text-fig. 5o). There seems little doubt that their season is related to the seeding of the grasses, which is at its height some time after the rains start, in May.

In *Volatinia*, for which there are most records, moulting birds were trapped in every month from August to February (with the exception of September, when only one bird was trapped); in the months March-July, none of the 32 birds examined was in wing moult. The fewer records that were obtained for *Sporophila* species showed moult in most months from June to February, and none in the months March-May.

Saltator coerulescens, a much larger and ecologically distinct species, probably feeding much on insects and to some extent on soft fruit, has a breeding season similar to that of the tanagers, at its height from April to July, and moults from August to January.

Local Differences within Trinidad

The considerable differences in climate within Trinidad would be expected to be associated with corresponding local differences in breeding season. In particular, breeding seasons would be expected to be shorter and more confined to the wet season in the northwest part of the island, where the rainfall is low and the dry season correspondingly severe, than elsewhere. As already mentioned, the bulk of the data on which this paper is based were collected in the Arima Valley in the central part of the Northern Range, near Arima itself, and in the Sangre Grande area some 15 miles to the east. Consequently we have not enough records from different areas for a proper examination of local differences, but such

Table XIII. Breeding and Moulting of Seedeaters

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Number of species breeding	2	—	—	—	3	5	5	4	4	1	3	3
Number of species moulting	2	2	—	—	—	3	—	2	1	1	2	3

as they are, they provide some evidence for the differences that would be expected.

As mentioned earlier, *Troglodytes* was found nesting in all months in the Sangre Grande area, but not in the Arima Valley, where its season was divided into two main periods, with a period of inactivity in the middle of the dry season and another in July-August. Likewise, *Columbigallina talpacoti* was found breeding almost continuously in the Sangre Grande area, but at Arima it ceased for the last few weeks of the dry season.

In each of the three years when nests were searched for, *Manacus* was found to start breeding considerably earlier in a valley about ten miles to the east than in the Arima Valley, in one year about six weeks earlier (Snow, 1962a). Wet weather is one of the external factors stimulating breeding in *Manacus,* as in other species (p. 25), while drought inhibits breeding, so that it is likely that towards the dry western end of the Northern Range there is an increasing tendency for birds to delay breeding until the onset of the wet season.

Breeding probably begins earlier at high altitudes in the Northern Range than in low-lying areas near by. Belcher & Smooker make the same generalization, but without supporting evidence; we had evidence only for *Elaenia flavogaster.* Of ten nest records from 1,200-1,800 ft. in the Northern Range, one each was in November, December and February, and the rest in April-June. None of the other 29 records from low altitudes was earlier than March. The reason for this difference remains obscure.

We had no breeding records from the very dry islands off the northwest corner of Trinidad, but visits at several times of year gave evidence of almost complete quiescence at the height of the dry season, followed by an outburst of song in April, just before the onset of wet weather. The state of the vegetation also suggested that, except perhaps for hummingbirds and *Coereba,* breeding in these islands must be mainly confined to the wet season. Since a day of intensive trapping in mid-October on Chacachacare, the driest and westernmost island, showed that many birds were in moult, as elsewhere at that season, we conclude that for most birds the breeding season there is short, lasting from May to September.

Differences According to Habitat

We have no data enabling us to test the effect of habitat on the breeding season of any individual species, except for the hummingbirds *Glaucis hirsuta* and *Amazilia tobaci.* As already mentioned, we found that both these species began breeding earlier in open places than in the forest. At least in *Glaucis,* the difference appeared to be related to the later appearance in the forest of the flowers on which it fed.

But interspecific comparisons afford some, though rather weak, grounds for supposing that breeding seasons are longer in open and semi-open country than in the forest, as has been found elsewhere in the tropics (Tanganyika, Moreau (1950); British Guiana, Davis (1953)). In the first place, all the species found to have continuous breeding seasons are characteristic of open habitats (*Columbigallina talpacoti, Crotophaga ani, Troglodytes musculus, Thraupis palmarum*). Differences in breeding seasons within two of the largest families, the flycatchers and tanagers, also provide some supporting evidence. As already mentioned (p. 12), the flycatchers of open country tend to have longer breeding seasons than the forest species. The tanagers most characteristic of open country, *Thraupis palmarum, T. virens* and *Ramphocelus carbo,* have longer breeding seasons than *Habia rubica* and *Tanagra violacea,* primarily forest species. However, inadequate knowledge of the breeding seasons of the species most strictly confined to forest (*Tangara gyrola, T. chrysophrys, Thraupis cyanocephala* and *Piranga flava*) makes this conclusion doubtful. The breeding seasons of the *Turdus* species run contrary to the generalization, *T. nudigenis,* the savanna species, having a much shorter season than *T. fumigatus* and *T. albicollis,* the two forest species. As pointed out earlier, there is an obvious reason why ground-feeding birds like thrushes should be able to breed for a greater part of the year in the forest than in open country. Finally, almost complete ignorance of the trogons and most of the antbirds, preeminently forest species, further weakens any generalization, especially as the little evidence we have suggests that they have very long breeding seasons.

If all species are taken together, the difference between the breeding seasons in forest and the various types of open and semi-open country

Table XIV. Breeding Seasons of *Pipromorpha oleaginea* in Five Years
(Number of nests started in half-monthly periods)

	1957	1958	1959	1960	1961
February 1				(B)	
February 2				(2B)	
March 1					
March 2		1			
April 1				(B)	
April 2		3	2		
May 1	1	1	4		
May 2	2		5	3	
June 1	4	1	4	2	3
June 2	2		4		2
July 1			1	2	2
July 2	1				2
August 1	1				1
August 2					
September 1	1				

Notes: Nests from the Arima Valley only are included. B: nest being built, but abandoned before completion.

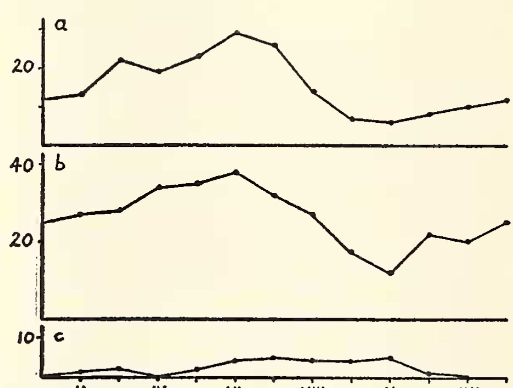
(except swamps) is not striking (Text-fig. 6). The only difference in breeding season according to habitat which is outstanding has already been mentioned and discussed in earlier sections; as Text-fig. 6 shows, the peak of breeding of the swamp species is from June to October, about three months later than the peak in other habitats.

Annual Differences in Breeding Season

Most species for which adequate numbers of nests were found in two or more years showed rather little annual variation in their breeding season. Thus no significant variation was found in the onset or duration of the breeding season in the swifts *Chaetura brachyura* and *Cypseloides rutilus* in five years, the thrushes *Turdus fumigatus* and *T. albicollis* in five years, or in *Coereba flaveola, Turdus nudigenis* and *Ramphocelus carbo* in three years, though larger numbers of records would doubtless have revealed small differences. In all of these, the breeding season in each year was much the same as for all years combined. The same was probably true of other species of which few nests were found in any one year, but whose song periods were rather constant from year to year *(e.g., Xiphorhynchus guttatus).* In the hummingbird *Glaucis hirsuta,* the time of onset of breeding varied by about a month in different years, and the beginning of the song periods of *Phaethornis longuemareus, Amazilia chionopectus* and *Colibri delphinae* showed a similar amount of variation. (For *Glaucis,* the comparison here is between birds nesting in the same habitats; it has already been mentioned that nesting begins later in forest than in open habitats).

The greatest annual variation in breeding season was found in *Manacus.* In the Arima Valley, the date of onset of breeding varied by five months, from early January to early June, in the five years of study (Snow, 1962a). The proximate factors involved were not clear. The beginning of breeding bore no fixed relation to changes in weather, though severe drought was found to inhibit breeding. It seemed that varying feeding conditions also exerted an effect. *Manacus* normally begins to breed during a period of increasing dryness and gradually increasing fruit supply, but conditions vary from year to year. It seems that in the Arima Valley the inhibiting effect of drought and the stimulating effects of increasing food supply are nicely balanced, so that slight changes in either can lead to large differences in the onset of breeding.

Although records were rather few in each year, *Pipromorpha oleaginea* also showed rather large variations in the beginning of breeding in the five years of study (Table XIV); in each year, the period of calling of the males agreed so closely with the periods when nests were found that there is little doubt that the observed differences are reliable. The variations agreed to a limited extent with those in *Manacus* in the same years. Thus in 1960, which was a very early season for *Manacus, Pipromorpha* started to call and build nests much earlier than in any other year, but none of the nests that were found were completed and there was an inactive period of about a month before nesting began again. *Pipromorpha* and *Manacus* would be expected to show some agreement in their response to proximate factors affecting breeding, as they occur in the same habitats and both nest mainly along streams, and both feed on fruit and insects,



Text-fig. 6. The breeding season in (a) forest, (b) open and semi-open country, and (c) swamps; as shown by the numbers of species found breeding in each month.

though *Manacus* is much the more specialized fruit-eater.

In view of the variability in *Pipromorpha's* breeding season, it is of especial interest that individuals were found to show very little variation in the dates on which they began to moult in different years (p. 23). In this they differed from *Manacus,* which showed much greater annual differences in the moult dates of individuals, though not nearly such great differences as in the time of onset of breeding.

In *Steatornis,* the only other species for which we have data, the date of onset of breeding was found to vary by about three months in different years, from December to late March (Snow, 1962 (1963)d). No satisfactory explanation could be suggested for the particular differences which were found, but two considerations are relevant. The nesting cycle of this species is very long, so that it may be impossible for a pair, if it has had two broods in close succession, to nest again at the same time in the following year; and since the species is highly social, the start of breeding tends to be synchronized in a colony.

Number of Broods per Year and Intervals Between Broods

In nearly all the species for which we have information, a complete nesting cycle, from nest-building to the fledging of the young, is far shorter than the extent of the annual breeding season. In most, several complete nesting cycles could be fitted into the season, and it is of interest to know how many nesting attempts are in fact made. Without such information we cannot fully understand the tropical breeding season, nor compare the reproductive rate of tropical species with their counterparts in temperate regions. We were able to collect data on this head for several species, especially those that habitually re-use the same nest or build another close to the previous one.

Turdus species

In the thrush *Turdus fumigatus,* on the basis of re-use of nests and also from observations on color-ringed birds, it was found that three or four broods may be reared in a year (Snow & Snow, 1963). In the months April-July, relaying followed rather soon after the end of the previous nesting attempt, or else there was a very long gap, doubtless because the moult intervened. In the months December-February, the intervals were mostly rather long, but variable, corresponding to the erratic and low incidence of breeding during the dry season (Table XV).

In *T. nudigenis,* whose breeding season is only three months long, there were two records of the re-use of the same nest, the intervals being 10 and 15 days. The breeding season is hardly long enough for more than two broods to be reared. Haverschmidt (1959) gives records of four broods reared in the same nest of *T. leucomelas* in Surinam, where the species has a breeding season of about eight months, the intervals being 18, 8 and 12 days.

The shortest intervals between broods, of 15 days or less, are of about the same length as the usual intervals in the European Blackbird *(T. merula),* which usually makes 2-4 nesting attempts within a breeding season of about four months (Snow, 1958). *T. nudigenis,* with a breeding season of about three months, almost certainly makes on average fewer nesting attempts than *T. merula* in England, while *T. fumigatus,* because of the very long intervals between broods in the dry season, makes about as many attempts in spite of having an almost continuous breeding season.

Manacus manacus

In *Manacus,* the breeding season varied in length from four to eight months in the five years under study. Each female made as a rule two or three nesting attempts in the shorter seasons, and more often three or four in the longer seasons. Intervals between broods were variable, (Table XV), at least partly in relation to favorable or unfavorable environmental conditions (Snow, 1962a).

Thraupis palmarum

For this species, the intervals between successive nesting attempts could be determined for the birds, already mentioned, that nested (one pair per tree) in three ornamental palm trees in the Arima Valley. Of the 20 intervals, 12 were between 11 and 25 days, and the other eight all much longer (Table XV). Nesting was especially successful in one of the trees, which had 19 of the 35 nests. From Text-fig. 7, which shows the succession of nests in this tree graphically, it will be seen that there was generally a rather quick succession of nesting attempts from March to August, then a gap during which the birds presumably moulted (this being the moult season for the species). In three of the four years there was then a single nesting attempt in October or November, followed by a rather long gap until the next attempt in February or later. The seasonal distribution of nests in this one site matches that of the combined records quite closely, so that the intervals too are probably typical of the species as a whole.

Troglodytes musculus

For *Troglodytes,* six intervals were deter-

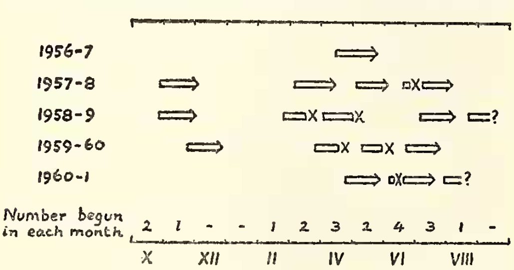
Table XV. Intervals Between Successive Broods in Twelve Species

	Number of days between ending of one nesting attempt and laying of first egg of next clutch									
	0	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41+
Columbigallina talpacoti	—	1	1	1	—	—	1	1	—	—
Steatornis caripensis	2	—	—	—	3	6	—	1	—	35
Chaetura brachyura	—	1	3	3	5	3	3	5	—	4
Cypseloides rutilus	1	—	4	2	—	1	—	—	—	—
Glaucis hirsuta	—	—	—	1	1	6	1	3	1	1
Anthracothorax nigricollis	—	—	1	—	1	1	1	—	1	1
Amazilia tobaci	—	—	—	1	1	—	1	—	—	—
Manacus manacus	—	1	1	7	3	6	2	6	4	9
Troglodytes musculus	—	—	—	—	—	—	—	—	—	6
Turdus fumigatus	—	—	3	2	4	—	1	2	1	8
Turdus nudigenis	—	—	1	1	—	—	—	—	—	—
Thraupis palmarum	—	—	—	5	3	4	—	—	—	8

mined for a pair which nested behind the ventilator above a window for over four years, from March 1957, to September, 1961. It was not certain that the same female survived for the whole of this period; in fact there was probably a change of female in early 1959; but it is safe to assume that most of the intervals are between successive nestings of the same female, and certainly that there was continuity of one member of the pair between every interval. The sequence of nests was rather similar to that of *Thraupis palmarum* in that in each year the birds started to nest between late October and early December, presumably soon after they had finished moulting. But thereafter the intervals between nests were much longer, especially in the middle of the dry season; there was none of less than 40 days, and only two or three nesting attempts were made in the year (3, 2, 2 and 3 in the four years). The sequence is shown graphically in Text-fig. 8.

Hummingbirds

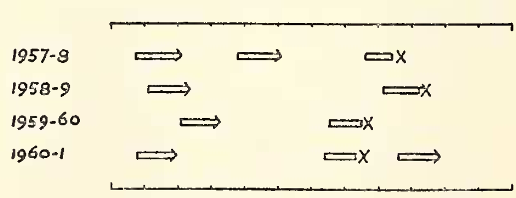
Information is available for three species of hummingbirds. *Anthracothorax nigricollis* was found to nest two or three times in the season (five records; 2, 2, 3, 3, 3), and for *Amazilia tobaci* there was one record of three successive broods and several of two broods in the season. For both species, the intervals between broods were variable, but few of them were very short (Table XV). For *Glaucis hirsuta,* 14 intervals were recorded between broods in the same nest, and these also were variable and mostly rather long. Because of the abundance of this species along the streams where it nests, the building of a new nest very near to an old one that had been used shortly before could not safely be ascribed to the same bird, so that the number of nesting attempts per year could not be ascertained, but 2, 3 or occasionally 4 seemed to be the rule.



Text-fig. 7. The succession of nests of *Thraupis palmarum* in a single palm tree, 1957-1961. Each nesting attempt is represented by an arrow, if successful, or by a rectangle followed by an X, if unsuccessful.

Swifts

Chaetura brachyura, the species for which most information was collected, was found to make from one to three, occasionally four, nesting attempts within the breeding season, which lasted about four months (Snow, 1962b.) Nest losses were high in the colony under study and the number of nesting attempts was almost certainly higher than it would be in a more successful breeding population. None of the pairs which were successful with their first brood



Text-fig. 8. The succession of nests of *Troglodytes musculus* in a single nest-site, 1957-1961. Conventions as in Text-fig. 7.

made more than one further attempt in the same season. The situation was similar in *Cypseloides rutilus,* but breeding success was higher and the average number of nesting attempts consequently lower, although intervals between successive nesting attempts were on average shorter (Table XV).

Steatornis caripensis

The nesting regime of *Steatornis* is peculiar (Snow, 1962 (1963)d). Each nesting cycle is very long, lasting nearly six months. Two may just be completed within one year, and there were a few records of this and even of three being completed in 18 months. These quick successions were then followed by long intervals of many months.

During the months when most clutches were laid (December-May), it was usual for laying to follow rather quickly after the ending of a previous nesting attempt, giving the short intervals shown in Table XV, but nesting attempts ending in the other months of the year were usually followed by intervals of four months or more.

Columbigallina talpacoti

For this dove there was a record, unfortunately unsupported by precise dates, of a succession of five broods in the same nest, and three records of two broods being reared in the same nest. In addition, Junge & Mees (1958) record a succession of three broods in one nest. Three of the five known intervals between successive attempts were short (2, 10, 14-15, 28 and 33 days). For the same species in Surinam, Haverschmidt (1953) records intervals of 13 and 34 days. These intervals suggest that within its almost continuous breeding season there tend to be quick successions of broods during favorable periods, followed by long intervals when conditions become less favorable. The opportunist nature of this dove's breeding is discussed elsewhere in relation to its breeding season and moult (p. 5).

To summarize, all the species discussed above regularly make more than one nesting attempt in the course of the breeding season. The number of attempts depends partly on the length of the breeding season, but is by no means proportional to it, since in those species with very long breeding seasons there tend to be very long intervals between broods at certain times of the year. At least in some species *(T. fumigatus, Manacus, Troglodytes),* these long intervals occur at times of year which there is reason to suppose are relatively unfavorable for breeding; their effect is to produce a "trough" in the pattern of the breeding season, while the short intervals are associated with the "peaks."

Duration of the Moult in the Individual

There is little information available as to how long it takes for an individual bird of any species to complete its moult under natural conditions. For tropical land-birds, there seem to be only Miller's records for the Andean Sparrow *(Zonotrichia capensis),* which completes its moult in about two months with rather little variation either way (Miller, 1961); while Baldwin (1953), from a study of skins, suggested five months as the likely duration of moult in Hawaiian honeycreepers (Drepanididae). In the Oilbird, the moult almost certainly lasts at least six months (Snow, 1962 (1963)d), a period comparable to that taken by sea-birds *(e.g.,* 7 months for *Anous stolidus*—Ashmole, 1962). With such wide potential variation, it is important, for an understanding of the annual cycle, to have some idea of the usual duration of the moult in the species with which we are concerned here, especially those with very long or continuous breeding seasons.

Repeated trapping of the same individuals gave us some information on this head for eleven species. The fullest data are on *Manacus,* of which seven individuals were trapped more than once in the course of a single moult. From the progress made between successive trappings, it was found that, except for the innermost and outermost feathers, two or three of which drop more or less together, the primaries drop at intervals of 8-10 days and the complete replacement of the primaries must take about 80 days (Snow, 1962a). This agreed exactly with the length of absence of individual adult males, while moulting, from their courts at the display ground, which was known accurately in nine cases to be between 76 and 85 days.

Less complete information was obtained for several other species, and is given, with that for *Manacus,* in Table XVI. Except for *Steatornis,* which is exceptional in the slowness of its moult as of its breeding, the figures show good general agreement. In the two piciform species, *Celeus elegans* and *Momotus momota,* the progress of primary moult was at the rate of one feather per 16 days, while in the passerines the rates were mainly around one feather per 8-10 days, giving estimated total durations of around 90 days. This agrees well with our only two records for complete moult periods. An individual of *Turdus fumigatus,* trapped just as it was beginning its moult, had very nearly finished it 91 days later, and an individual of *Pipra erythrocephala,* trapped when it was just beginning to moult, had completed its moult 96 days later.

TABLE XVI. RATE OF PROGRESS OF WING MOULT IN TEN SPECIES

	Number of primaries replaced between captures	Primaries replaced (numbered from inside)	Interval in days	Rate of moult: number of days per primary
Momotus momota	6	2-7	96	16
Celeus elegans	4	3-6	65	16
Xiphorhynchus guttatus	2	3-4	14	7
Dendrocincla fuliginosa	3	1-3	45	15
Manacus manacus	9	1-9	79	9
Manacus manacus	7	3-9	59	8
Manacus manacus	3½	1-4	27	8
Manacus manacus	3	3-5	25	8
Manacus manacus	3	4-6	25	8
Manacus manacus	1¾	3-4	21	12
Manacus manacus	1½	1-2	12	8
Pipra erythrocephala	3	3-5	20	7
Pipra erythrocephala	1¾	2-3	13	7
Pipromorpha oleaginea	2	6-7	19	10
Turdus fumigatus	3½	6-9	50	14
Tachyphonus rufus	3	3-5	22	7
Ramphocelus carbo	5	2-6	73	15
Ramphocelus carbo	3½	1-4	28	8
Ramphocelus carbo	2	2-3	28	14

Other things being equal, the greater the number of adjacent primary feathers being replaced at the same time, the more quickly will the wing-moult be completed. In fact, in many species considerable individual variation was found in the number of adjacent feathers growing at the same time, and for all individuals the number tends to be larger in the early and late than in the middle stages of the moult. In *Manacus* and *Pipra,* two or three were the usual numbers. In *Celeus,* whose moult probably takes longer, one or two adjacent feathers only were found growing at the same time. In *Thamnophilus* and *Columibigallina talpacoti* it was unusual for more than one primary in each wing to be growing at the same time. It will be recalled that in these two species both the breeding and moult seasons are more or less continuous, and there is doubtless a connection between the ill-defined annual cycle and the fact that their moult is a slower process than in species with better defined annual cycles.

Tanagers of the genus *Tangara* also seem to have a very slow moult, and in this respect, as in their season of moult (p. 15), to stand somewhat apart from their relatives. In them too it was found to be unusual for more than one primary to be growing at the same time in each wing (one primary in ten instances, two primaries in three instances); whereas in other tanagers, though there is considerable variability, it was more usual to find two adjacent feathers growing simultaneously than any other number, and three or four were not uncommon. In *T. gyrola,* the only individual that was trapped twice while moulting gave evidence of a very slow rate of moult. The two primary feathers that were growing at the time of the first capture (6th primary in each wing, ¾-grown and nearly full-grown respectively) were still not full-grown 15 days later and no other feathers had fallen. (This individual is omitted from Table XVI, as the rate of moult cannot be calculated in this case). In addition, two individuals of *T. gyrola* showed a condition of arrested moult similar to what was found in *Columbigallina talpacoti* (p. 5). However, in spite of this evidence for a slow rate of moult, the total duration of the moult season of *Tangara* species is not particularly long (Text-fig. 5n), which suggests that the moults of the individuals within the population may be better synchronized than in the other tanagers. Clearly the annual cycle in *Tangara* would repay more detailed study.

INDIVIDUAL AND ANNUAL VARIATION IN THE SEASON OF MOULT

If about three months must be allowed for the moult in typical small or medium-sized passerine birds, and longer periods for the larger birds, as the above figures suggest, a continuous or nearly continuous breeding season is possible only if the annual cycles of the different individuals in the population are not very exactly synchronized. An alternative possibility is that individuals may moult while breeding, but our evidence suggests that in at least most of the species with which we are concerned this is not so. We had enough re-traps of different individuals moulting in the same year, and of the same individuals during their moults in different years, to show that there is, as would be expected, enough individual and annual variation to account for the overlapping breeding and moulting seasons that were in fact found.

Nine individuals of *Manacus* were trapped while moulting in two or more different years. They showed variations of up to 78 days in the calculated dates of onset of their moults in different years, though in five of the eight comparisons that could be made between successive years the difference was 26 days or less. The dates on which color-ringed adult males disappeared from their courts at a display ground for their moult, and re-appeared after the moult, showed similar annual variations (Snow, 1962a). Records for four individuals of *Pipra erythrocephala* showed smaller annual variations—a maximum difference of 39 days between different years, and differences of 12, 21 and 26 days between successive years.

The records for four individuals of *Pipromorpha oleaginea* show surprising constancy from year to year, the calculated dates of the start of moult being as follows:

	1958	1960	1961
Bird no. 1	July 4	July 18	July 11
Bird no. 2	July 4	—	July 13
Bird no. 3	—	Aug. 7	Aug. 11
Bird no. 4	—	June 27	June 28

In addition to these three species, single individuals of five other species were trapped in moult in two successive years: *Xiphorhynchus guttatus, Myrmotherula axillaris, Leptopogon superciliaris, Dacnis cayana* and *Tachyphonus luctuosus.* Allowing for the probable rate of moult, all proved to have started their moults at about the same date in both years.

The General Pattern of the Annual Cycle

Text-fig. 9 shows the breeding and moulting seasons of all the species combined, by summation of the numbers of species found breeding and moulting in each month. Of course the picture produced by such treatment of the data is of limited significance, though for lack of any better means it has had to be used in many studies of tropical breeding seasons. In the first place, even if one's information were complete for every species, the pattern so obtained would not correspond to any one actual breeding or moulting season, being derived from numerous species with widely varying seasons. Secondly, the information is in fact far from complete, so that the shape of the pattern is much affected by chance variations in the contributions made by the different species, according to their abundance or rarity and the ease with which they can be trapped or their nests found. Thus if the information were much better for the hummingbirds than for the seed-eaters (as is the case), the breeding curve would be too high in the early months of the year.

Text-fig. 9. The general breeding season and moulting season of Trinidad land-birds. Solid line: number of species found breeding in each month. Broken line: number of species found moulting in each month.

Accepting these limitations, we can nevertheless safely take the months April-June as the height of the breeding season in Trinidad. In these months nearly all the species of land-birds are breeding—the early ones have not quite finished, the late ones are just starting, and most of the others are in the middle of their breeding season. To this can be added the further generalization, that moulting is at its height in the months July-October.

Whether, within this broad pattern, any individual species or group is early or late, or has a long or a short breeding season, can in many cases be explained on the basis of its ecological requirements. The evidence on this head for the oilbird, hummingbirds, swifts and swallows, nightjars, manakins, bananaquit, icterids and seed-eaters has already been given in the preceding sections. The swamp-inhabiting species, as a group, are another good example; the reason for their late breeding season has also been discussed (p. 12).

There remain a number of species with continuous or nearly continuous breeding seasons. A few, such as *Columbigallina talpacoti, Crotophaga ani* and *Thamnophilus doliatus,* appear to be emancipated from a fixed annual cycle and to both breed and moult in any month. But most of them, as far as known, moult at the same time of year as the other species. This is certainly so for the tanagers *Thraupis palmarum* and *T. virens* and the thrush *Turdus fumigatus,* and probably so for *Pitangus sulphuratus, Turdus albicollis, Troglodytes musculus* and *Mimus gilvus.* It is difficult to believe that the single month or two in which these species do not breed is in some way unsuitable for breeding. The most reasonable explanation is that environmental conditions are suitable for breeding at all times of year, but that the birds have kept to an annual cycle which is adapted to conditions prevailing in neighboring areas with more seasonal climates.

The very long breeding seasons of the species mentioned above also have in common the fact that they are bimodal. Soon after the end of the moult, or the time when it may be presumed to have ended, there is a resurgence of breeding, reaching a peak usually in October or November. This is then followed by a decline, which in its turn is followed by a more gradual increase in activity leading to the second, main peak in May or June. The period of reduced activity, in all the species, coincides roughly with the first part of the dry season, but the decline itself cannot be a direct result of dry weather since it begins while the weather is still very wet, in November or December. Furthermore, the resurgence which leads to the May peak begins while the dry season is at its height. It seems likely that this double-peaked breeding season depends mainly on an internal rhythm, and is perhaps accentuated by the inhibiting effect of dry weather in January-March and low minimum temperatures in November-February (see also p. 26).

Reviewing the general pattern of the annual cycle of breeding and moult, one cannot fail to be struck by certain broad similarities between the annual cycles of Trinidad birds and those which prevail in the northern hemisphere generally. The peak of breeding is at approximately the same time, the moult is at much the same time, and there is an apparent analogy between the minor October-November peak of breeding in Trinidad and the autumn recrudescence of sexual behavior in northern birds. One is led to wonder whether these main events of the annual cycle in Trinidad are in fact "homologous" with the events in the north-temperate region in the sense that they pass gradually into one another in the intervening latitudes, and if so, to what extent they are controlled by the same proximate and ultimate external factors. These and related problems will be discussed in the following sections.

Ultimate Factors Controlling Breeding

In discussing the factors controlling breeding seasons it is helpful to distinguish between ultimate and proximate factors, as originally pointed out by Baker (1938). Ultimate factors are those which make breeding possible, or more likely to succeed, at one time of the year rather than another, and include especially, for birds, weather and the food supply for the young. These are the factors that ultimately determine at what time of year breeding takes place. Proximate factors are those factors in the changing environment to which the organism responds, and which act as the timers of the breeding season in the physiological sense. They need be themselves of no direct significance for breeding. The shorter the period between the beginning of breeding activities and the production of young, the more likely it is that ultimate and proximate factors will be closely related. Thus for a small bird the proximate factor may be rainfall, and the ultimate factor may be the increased food supply which immediately follows rainfall.

It has been shown for two specialized fruit-eaters whose diets show no overlap, *Steatornis* and *Manacus*, that most young are in the nest when the greatest variety of fruit is available, and in both species this period is in the months April-June. However, since their incubation and fledging periods are very different, their egg-laying seasons differ greatly. Two swifts, among the most specialized of the insectivores, start to breed at the end of April or early May, and there is good reason to believe that the early part of the wet season, from mid-May onwards, when most of their young are in the nest, is the period when insect life is at its most abundant. Thus both for specialized fruit-eaters and specialized insect-eaters the greatest abundance of food seems to be available in the same months of the year, and it is not surprising that this is the time when the breeding season of the land-birds taken as a whole reaches its main peak. Nor is it difficult to see the selective advantage gained by certain groups, of specialized habitat, diet or nesting habit, in breeding earlier or later than the others. These have been discussed in detail in earlier sections.

Hence it is a reasonable hypothesis that the breeding seasons are ultimately adapted to take advantage of the periods of greatest food supply and, in some species, to the period of greatest safety of the nest. That the seasons, thus evolved, reach their height in the main at the same time of year as the breeding season in the north-temperate region, can be regarded as a biological coincidence, resulting from the fact that the north-tropical wet season, determined by the northward movement of the equatorial low-pressure belt, and the northern spring, begin at about the same time. Both, of course, are determined by the northward movement of the sun's declination.[2]

The fact that the moult season in Trinidad shows a similar correspondence with the moult season in the north is more puzzling. Beginning as it does approximately in the middle of the wet season, it seems to restrict the breeding season unnecessarily. Those species which wait for the wet season before breeding would do better, one would suppose, to continue breeding longer and moult later. As it is, the length of the breeding season of each species seems to depend on how soon it can begin to breed before the wet season starts. Some, like *Turdus fumigatus*, begin as soon as the moult is over, in October or November of the previous year; others, like *T. nudigenis*, not until the following May.

No final explanation is possible at present, but it may be that in most habitats the food supply declines significantly, and perhaps sharply, in the course of the wet season, so that conditions for rearing young may deteriorate even though the general aspect of the environment is unchanged. That this is indeed so for the fruit-eating birds is suggested by the data for both *Manacus* and *Steatornis*. The variety of fruits eaten by *Manacus* was found to reach its lowest point in September, and for *Steatornis* the availability of fruits of Lauraceae, the main family on which the young are fed, declines sharply in July. For insectivores we have no equivalent data, but it is perhaps significant that in swamps, where the food supply might be expected to reach its peak later than in other habitats, the insectivorous land birds both breed and moult later than those in other habitats.

Proximate Factors

Rainfall

For most species, we can say little about the proximate factors controlling their breeding. Indeed, we were impressed during our field work by the way in which species would start to breed and be well synchronized, unassociated with any clear environmental change. The few indications that we had were connected with the onset of the wet season. Discussion of other environmental factors is mostly speculative.

In 1959, very dry weather prevailed until April 9. Heavy rain fell on the 9th and 10th and immediately afterwards birds of several species were seen carrying nest-material. The first eggs of the season of *Manacus* were found ten days later, and four nests of *Turdus fumigatus* had eggs 9-13 days later, after a gap of nearly two months during which none had been found. In 1961 the wet season began late. There was some rain on May 22, but it then became very dry again for a week and wet weather did not properly start until May 28. As in 1959, it was followed by an outburst of breeding. The first eggs of *Turdus fumigatus*, which had stopped breeding and singing for several weeks, were recorded on June 6, and *Manacus*, which had practically stopped breeding since April, had a great resurgence of egg-laying in early June.

In other years, the first wet weather in April or May was not followed by any conspicuous outburst of laying. It can hardly be doubted that the more seasonal the climate and the more severe the dry season, the more important rainfall is likely to be as a proximate factor stimulating breeding. Many studies in arid regions have shown this, and in northern Venezuela, only a short distance to the west of Trinidad but with a considerably more seasonal climate, Gilliard (1959) describes how the onset of the rains has a spectacularly stimulating effect on breeding. It is reasonable to conclude that in the Arima Valley, and probably even more in eastern Trinidad where the climate is wetter, it is only one of several factors and in some years not an important one. Thus for *Manacus*, though under certain conditions rainfall is a proximate factor, as mentioned above, breeding usually begins before the wet season starts and its time of onset is probably determined in part by the varying state of the food supply, which increases in abundance during the first four months of the year; and it may even be affected by the availability of the material used for the lining of the nest (Snow, 1962a).

Day-length

There is still no general agreement as to the role of day-length as a proximate factor controlling breeding seasons in the tropics, where seasonal changes are very small; its importance in temperate latitudes has been amply proved. Recent experimental work has shown that the gonads of tropical and even equatorial birds, which in nature experience no change of day-length, may be stimulated by increasing light (*e.g.*, Marshall & Disney, 1956; Miller, 1959). Uncertainty remains as to how far towards the Equator the diminishing seasonal changes of day-length continue to have an effect, and as to

[2] Discussion of fresh-water and sea birds is beyond the scope of this paper, but it may be pointed out that the breeding seasons of herons and egrets, ibises, terns, and pelecaniform birds in Trinidad and Tobago are also at their height at the same time, although their ecological requirements are diverse and quite different from those of the land birds. The degree to which their breeding seasons are adjusted to environmental conditions would repay study.

their importance relative to other environmental factors.

Baker (1939), investigating the breeding seasons of a large number of Old World birds from all latitudes, found that April and May, the months of the northern spring, are still the favorite months for egg-laying at latitudes 0-10° N. Correspondingly, at latitudes 0-10° S., September is the favorite month. He suggested that the main proximate factors stimulating breeding in the tropics are, not day-length, but increased light intensity, associated with the overhead sun, and/or wet weather, while length of day and temperature are the most important proximate factors in temperate and boreal latitudes.

Moreau *et al.* (1947), investigating the annual cycles of three species at Amani, 5° S. in East Africa, found that their laying seasons were all more or less the same, October-January. The three species are ecologically so different that they could suggest no reason why it should be most advantageous for all of them to breed in the same months, which, as they pointed out, are "the central breeding months of the Amani bird fauna as a whole, including such dissimilar species as hornbills, rock-martins and bulbuls, and moreover, generally speaking, those of species at higher latitudes throughout the southern hemisphere."

Later Moreau (1950) pointed out that in Africa the breeding seasons begin in general with increasing day-length, but that this is also the time of increasing warmth, onset of the wet season and recrudescence of the vegetation, as it is also at 10° N. in Trinidad. Clearly, broad regional surveys of breeding seasons are of limited value in elucidating the role of individual proximate factors which are thus causally linked together in the main march of the seasons.

In more recent discussions, dealing more specifically with the neotropical region, Miller (1959 and 1960) has suggested that day-length is a significant proximate factor at 10° N. in Central America, and even further south. Miller concludes: "Thus at latitude 10° photoperiodic influences are clearly felt and probably these prevail weakly even to latitude 5°. Certainly they are far from absent at 8° in Panamá." However, Miller bases his conclusion simply on the fact that the peak of the breeding season comes shortly after the spring equinox, when day-length is increasing most rapidly, and does not seem to take full account of the environmental changes associated with increasing day-length, which, as in Trinidad and in the area studied by Moreau, include the onset of wet weather.

Our data lead to the conclusion that day-length is of little importance as a proximate factor initiating breeding seasons in Trinidad. Table XVII gives an analysis of the months of start of breeding in those species whose breeding seasons were known sufficiently accurately. Nearly one-third of them begin to breed when day-length is decreasing, and only just over one-third in the months (March-May) when it is increasing fastest.

Table XVII. Month of Start of Breeding of Sixty-two Species

(Only those species are included which have a limited breeding season that is known sufficiently exactly)

Month	Number of species starting to breed
January	10
February	7
March	8
April	10
May	3
June	5
July-August	—
September	1
October	5
November	6
December	7

It is thus clear that, whatever the role of day-length, it can have no very general effect in initiating breeding, or else changes in day-length must affect different species, including closely related species, in very different ways. If increasing day-length is responsible for the main peak of breeding, in April-June, as Miller concludes for Central America, its effect on most species must be to cause an increased amount of nesting in the course of a breeding season which has already begun, in some cases months earlier. One of the ways in which it would have to exercise this effect would be by causing re-nesting to follow more rapidly after the end of a previous nesting attempt, as in *Thraupis palmarum* (p. 19) and other species. Conversely, decreasing day-length might be one of the factors responsible for the "winter" decline in nesting which is usual in species with very long breeding seasons. We have no means of testing these hypotheses with the data at hand.

Temperature

Another physical factor which varies seasonally and more or less regularly is temperature. Again, as for day-length, it is unlikely that it can have any general effect in initiating breeding seasons, yet it is possible that, like decreasing day-length, it may play a part in the "winter" decline in breeding. It has already been shown that this decline, which leads to a low level of breeding in the first half of the dry season, cannot be a direct effect of dry weather, as it begins in November or December, while the weather is still very wet. But these are the months when temperatures, and especially the nightly minima, decline quite sharply, and they continue low until March, when they rise equally sharply (Text-fig. 3). It seems reasonable that this period of low minimum temperatures might have the same depressing effect on breeding activities as cold weather in the north.

It must be admitted that the little data that we have to test this suggestion do not lend it much support. Temperatures in the period November-February varied considerably in the three years 1958-59, 1959-60 and 1960-61. The breeding of *Turdus fumigatus* and *T. albicollis,* the only species with long breeding seasons of which enough nests were found for analysis, also varied in the same periods, but not in apparent relationship to the temperatures.

Internal Factors

In species which breed practically throughout the year, the beginning of breeding is probably determined internally, with the recrudescence of the gonads after the moult. Thus *Turdus fumigatus* starts to breed as soon as it has finished moulting and continues until its next moult starts. For such species the role of proximate factors, insofar as they affect breeding, must be limited to inhibiting and re-stimulating breeding within a more or less continuous season.

Most species wait a certain length of time after the end of the moult before beginning to breed. It has already been sufficiently stressed that it is hard to identify proximate factors stimulating breeding in such species, yet they tend to have definite and well synchronized breeding seasons. In the light of Marshall's recent work on the adaptive nature of differences in post-breeding refractory periods in the gonad cycles of different species of birds (Marshall, 1960), it seems likely that the length of time which elapses between the end of the moult and the beginning of breeding depends primarily on specific refractory periods, and is modified by environmental factors which sometimes may be obvious (time of onset of wet season) but more often are too subtle to be apparent to the observer.

The Control of the Annual Cycle

The arguments outlined in the previous section indicate that the proximate factors affecting the onset and course of the breeding season are unlikely to be of primary importance in controlling the whole annual cycle. In the first place there are those species, already discussed, which breed more or less continuously except when moulting, and moult at the same time each year. Secondly, there are species with restricted and annually variable breeding seasons, which nevertheless moult at the same time each year (*e.g., Manacus, Pipromorpha*). There is a further consideration which is not conclusive but at least highly suggestive, that the breeding seasons of different species start in all months from October to May, or even later, yet practically all of them moult in the same months of the year.

All this suggests that the maintenance of the annual cycle from year to year must depend on the birds' response to some regularly recurring environmental factor or factors whose effect is to induce the onset of moult. There is another important consideration which points the same way. In those species with long breeding seasons —and they are the majority—young birds may be born in many different months of the year; yet in nearly all the species for which we have data the first full moult, which takes place in their second year, is synchronous or nearly so with the post-breeding moult of the adults. There is good evidence that this first complete moult, which thus brings the young bird into synchrony with the annual cycle of the adults, precedes breeding; certainly it does so in the males of manakins, tanagers and honeycreepers, which have distinct juvenile and adult plumages.

In north-temperate species there is experimental evidence that decreasing day-length may induce moult, but day-length is an unlikely controlling factor in Trinidad, as in most species the moult begins at a time when it is hardly altering at all, and in many species the early individuals begin to moult before and the later ones after the summer solstice.

In discussing the annual cycle of *Manacus* (Snow, 1962a), it was suggested that the beginning of the wet season may play some part in determining the time of moult. This suggestion was supported by the data on the annual differences in the time of onset of moult of banded individuals which were followed over two years or more. In 13 out of 17 cases the annual differences in the time of moult were in agreement with the differences in the time of onset of the wet season. On the present data we cannot go further than this; but it may be pointed out that the beginning of the wet season is the most marked seasonal change of the whole year, and is also fairly consistent in its timing from year to year, so that it is perhaps the most suitable environmental time-giver available.

It is unfortunate that our trapping was not continued long enough to provide data for a critical test of the effect of the wet season on the onset of moult in several species. A large-scale trapping program, continued over several years, could provide the necessary data, and would perhaps be more valuable at this stage than the accumulation of more and more breeding records.

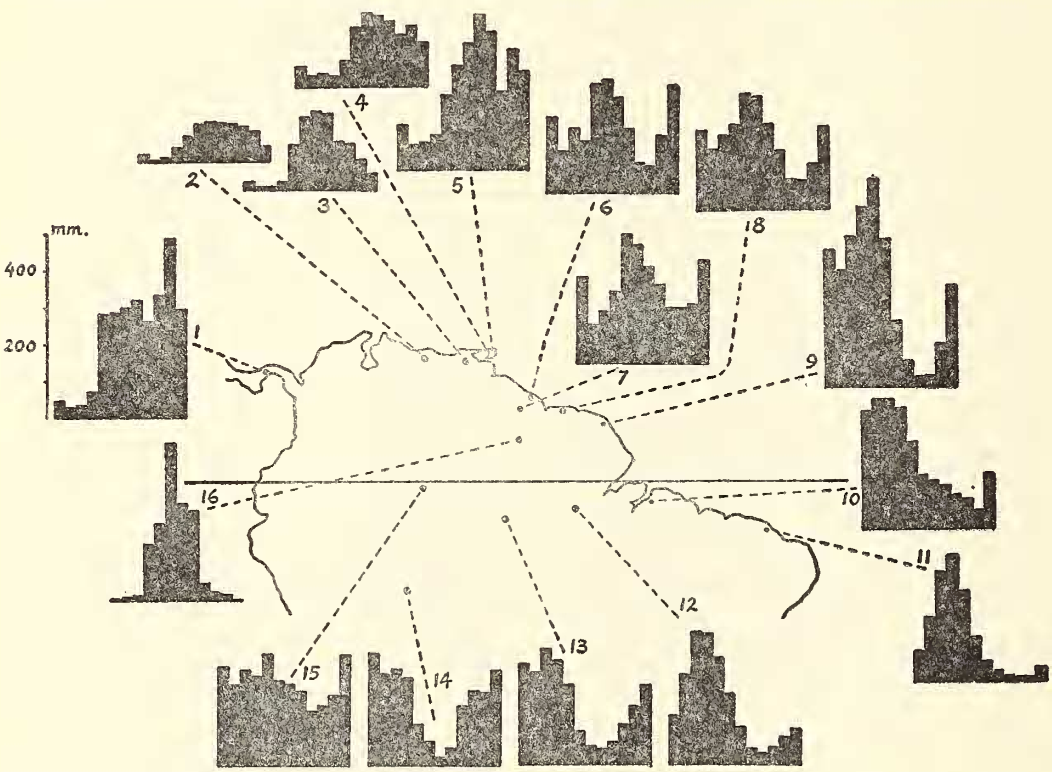
Trinidad in Relation to Northern South America

The Trinidad Climate in a Wider Context

The climate of Trinidad is broadly similar to that of northern Venezuela immediately to the west—a long dry season, from January to May, is followed by wet weather for most of the rest of the year. This regime is characteristic of northern South America east of the Andes and of much of southern Central America. (We shall not be concerned here with South America west of the Andes, where different climatic conditions prevail).

South of the Equator, at equivalent latitudes, the seasons are almost exactly reversed, or more accurately, shifted by six months—July to November are the driest months of the year, and January to June the wettest. This is the climate of the whole of eastern Brazil. From the present point of view, it is most instructive to consider the change-over from the south-tropical to the north-tropical rainfall regime as one proceeds northwestwards from the corner of Brazil along the coast of northern South America in the direction of Trinidad (Text-fig. 10).

The south-tropical regime remains unchanged as far as Belem, only 1° south of the Equator, except that the wet season begins slightly earlier, in December. The beginning of the change is seen at Cayenne, 4° N.; here the dry season in the second half of the year is restricted, and the wet season is beginning to be broken by a second dry season in February-March. At Paramaribo, in Surinam, the second dry season is more pronounced, and in northern British Guiana it is almost equal to the original dry season in extent, though not in severity. Northwestwards from British Guiana the dry season in the second half of the year rapidly diminishes and the February-



Text-fig. 10. The mean monthly rainfall at various localities in northern South America (all to the same scale, as shown for no. 1). Localities: 1, Barro Colorado, Panama. 2, Caracas, Venezuela. 3, Cantaura, Venezuela. 4, Port-of-Spain, Trinidad. 5, Arima Valley, Trinidad. 6, Georgetown, British Guiana. 7, Mazaruni, British Guiana. 8, Paramaribo, Surinam. 9, Cayenne. 10, Belem, Brazil. 11, Fortaleza, Brazil. 12, Taperinha, Brazil. 13, Manaos, Brazil. 14, Senna Madureira, Brazil. 15, San Gabriel, Brazil. 16, Lethem, British Guiana.

March dry season increases in extent and severity, until the rainfall regime shows the complete six-month shift from that prevailing in northeast Brazil. In Trinidad, a remnant of the July-November dry season still persists, as the "petit carême" already mentioned, being most apparent in the wetter eastern parts of the island. The rainfall of Port-of-Spain, near the northwest corner, is almost identical with that of adjacent northeast Venezuela and shows little evidence of the second dry season.

Inland in northern South America, the rainfall regimes characteristic of the coastal belt are much modified. The July-November dry season extends to much of the lower Amazon basin, but further inland it shifts to earlier in the year, until at Senna Madurera (9° 8′ S., 68° 40′ W.) the driest weather comes exactly in the middle of the year. Some areas are so wet that no dry season is apparent. The other main inland region, the savannas of central Venezuela and southern Guiana, has exactly the opposite rainfall regime. Here the northern dry season prevails, but its beginning comes earlier as one proceeds inland, so that at Lethem, for example, at 3° 18′ N., 59° 46′ W., wet weather prevails from April or May until August, the rest of the year being dry (Gilliard, 1962).

The rainfall regime of much of Central America, as already mentioned, is similar to that of Trinidad and northern Venezuela, with a wet season beginning typically in May and lasting for most of the rest of the year, but falling off in the last three months. As one proceeds further from the Equator and changes in temperature become more marked, this becomes a regime of dry winters and summer and autumn rainfall, such as is characteristic of most of Mexico.

To summarize, the climatic "Equator," at which the north- and south-tropical dry seasons are equally balanced, passes through the extreme north of British Guiana. Trinidad stands only 3 degrees north of it, at the point where the last trace of the south-tropical rainfall regime disappears, being obliterated by the north-tropical regime which from here to the west and northwest prevails over a huge area of northwest South America and Central America. As far as they are ultimately controlled by the wet and dry seasons, we should therefore expect the breeding seasons of Trinidad birds to resemble those of Venezuela and Central America, but perhaps still to be influenced by the double wet and double dry season regime which prevails only a short distance to the southeast.

The discrepancy between the geographical and what may be called the climatic Equator is very important in elucidating the factors controlling the annual cycle, already discussed with reference to Trinidad alone. For if day-length were the main proximate controlling factor, we should expect the half-way point in the shift from the northern hemisphere to the southern hemisphere breeding seasons to occur at the geographical Equator. If, on the other hand, rainfall exerts over-riding ultimate control, we should expect the shift to occur at the climatic Equator. If both exert an effect, we should expect some kind of intermediate condition. It will be seen from the following sections that the effect exerted by the rainfall regime is paramount, while that exerted by changes in day-length is open to question and in any case of minor importance.

The Breeding Seasons in Neighboring Areas

We have quantitative information, of varying fullness, on the breeding season in the following areas: Belem, northern Brazil (Pinto, 1953), and Cantagallo, eastern Brazil (Euler, 1867); northern British Guiana (Davis, 1953; also summarizing Beebe, 1925); northeast Venezuela (Friedmann & Smith, 1955); Costa Rica (Skutch, 1950). In addition, Haverschmidt has published details for several species in Surinam. (The extensive data given by Penard & Penard (1908-10) for Surinam are unreliable (Haverschmidt, 1949)). It will be most convenient to consider these areas in a logical rather than geographical order.

Northeast Venezuela. Friedmann & Smith's data, from an area of savanna and seasonal woodland only about 100 miles from Trinidad, show a sharp rise in breeding activity in March, coming to a peak from April to July, followed by a general decline from August to December which is interrupted by a minor resurgence in October (Text-fig. 11b). The peak is at the same time as in Trinidad, the breeding seasons of the main ecological groups are similar, and those species for which there are data from both areas show good general agreement. The main difference, as would be expected from the difference in climate, is that the breeding season appears to be shorter than in the Arima Valley; possibly it is no shorter than in the northwest corner of Trinidad. There is only one puzzling discrepancy between the northeastern Venezuelan and Trinidad records: *Amazilia fimbriata*, the only hummingbird for which Friedmann & Smith had many records, was found to breed from August to January, a season completely at varianee with that of any of the Trinidad hummingbirds.

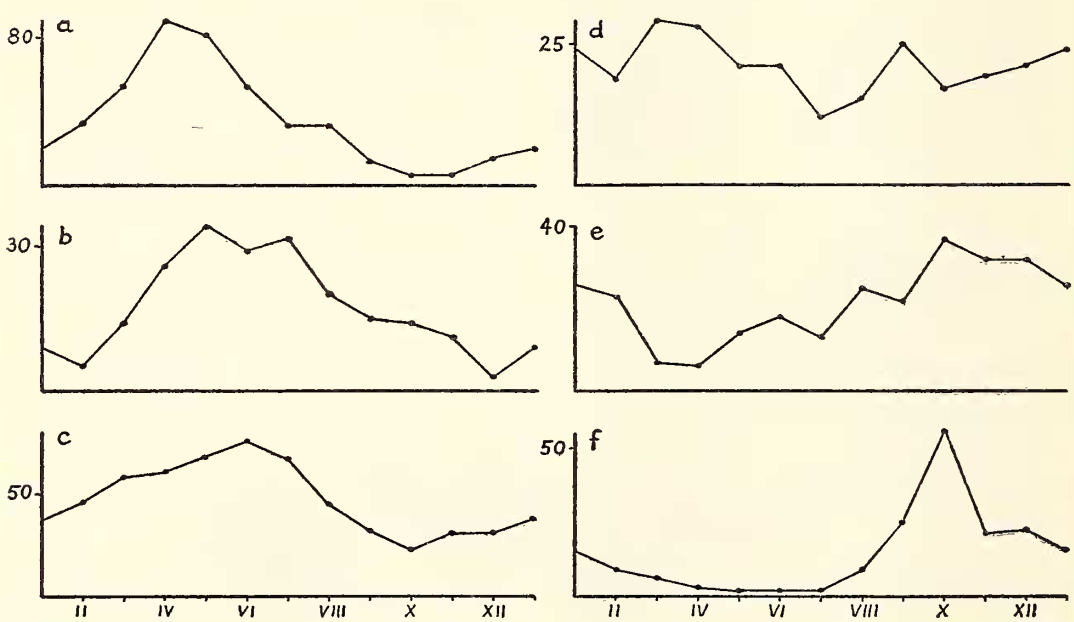
Central America. Skutch's extensive records, based on many years' residence, afford a far more detailed picture of the breeding seasons in

Central America than we have for the other areas reviewed here.

In general, there is a well-marked breeding season with its peak in the months April-June (Skutch, 1950, 1954, 1960). In the valley of El General in southern Costa Rica, where most of Skutch's records were obtained, the amount of breeding gradually increases through January, February and March, the driest months of the year, and reaches its maximum in April, just before the beginning of the wet season. Activity falls off from June to August, and in the last four months of the year there is very little breeding (Text-fig. 11a). A steady rise in breeding activity in the first four months of the year was found at a number of other localities and is doubtless general in Central America. Some groups of birds with specialized feeding habits breed at a different time from the majority, notably the nectar-drinkers and seed-eaters, and in each case Skutch was able to show a correlation with the season when their food was at its most abundant. He also gave convincing evidence that the time when most of the less specialized species were feeding their young (May-June) coincided with the time when the supply of insects and ripe fruit is at its height.

At low altitudes in Central America, the main peak of the breeding season and the associated environmental changes correspond closely with the situation in Trinidad (at high altitudes, as would be expected, the breeding season is more restricted). The chief difference seems to be in the seasonal abundance of flowers and, in association with this, the breeding season of the nectar-drinking birds. In the valley of El General flowers are most abundant in December and January, and least abundant towards the end of the dry season, in late March. Correspondingly, the hummingbirds and *Coereba* breed less in the second half of the dry season than at any other time, whereas in Trinidad the whole of the dry season is a period of abundant flowering and the nectar-eaters breed throughout it. At higher altitudes in Central America, also in agreement with the flowering season, Skutch found an even greater divergence in the breeding seasons of the nectar-drinkers from the general pattern. Thus in the Sierra de Tecpán, at 8-10,000 feet, their breeding was at its height in November and December.

It is noteworthy that, although the climate of the valley of El General is as wet as any part of Trinidad and it is a little nearer the Equator, the main peak of breeding is more sharply defined than in Trinidad, and there is no indication of a secondary peak in October or November. The difference is also apparent if the breeding seasons of species common to both areas are compared (Table XVIII). The climate of El General, for orographic reasons, is much wetter than that of neighboring areas (Skutch, 1950). It



TEXT-FIG. 11. The breeding seasons in central and northern South America (number of species found breeding in each month). (a) Costa Rica (Skutch, 1950). (b) Northeast Venezuela (Friedmann & Smith, 1955). (c) Trinidad. (d) Northern British Guiana (Davis, 1953). (e) Belem (Pinto, 1953). (f) Cantagallo (Euler, 1867).

TABLE XVIII. BREEDING SEASONS OF FOUR SPECIES IN COSTA RICA AND TRINIDAD

	Total nests	% of clutches started in different months											
		Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Tyrannus melancholicus													
Trinidad	33	3	6	9	21	18	12	21	9	—	—	—	—
Costa Rica	—	—	—	x	x	x	x	—	—	—	—	—	—
Elaenia flavogaster													
Trinidad	39	—	3	3	33	36	18	3	—	—	—	3	3
Costa Rica	44	—	—	9	41	32	11	5	2	—	—	—	—
Pipromorpha oleaginea													
Trinidad	61	—	—	3	11	30	36	15	3	2	—	—	—
Costa Rica	16	—	—	25	44	13	13	6	—	—	—	—	—
Thraupis virens													
Trinidad	111	7	4	9	28	19	18	10	1	—	3	1	1
Costa Rica	49	—	—	27	47	20	4	2	—	—	—	—	—

is tempting to suppose that the breeding season is adapted primarily to the drier conditions that prevail over the greater part of the Pacific slopes of Costa Rica, as discussed more fully later (p. 32).

Belem. In the neighborhood of Belem, only 1° south of the Equator, where the wet and dry seasons are almost exactly at the opposite time of the year from the seasons in Trinidad and northeast Venezuela, the breeding season is correspondingly shifted. Incomplete though Pinto's data are, they show that the period of greatest activity is from October to December, the end of the southern spring, and the period of lowest activity is in March and April (Text-fig. 11e). The peak of the breeding season coincides with the time when breeding is at its height at Cantagallo, 22° S., in the neighborhood of Rio de Janeiro (Euler, 1867; Text-fig. 11f), and presumably in all subtropical and temperate parts of South America south of the Equator. Pinto's data further show that the switch-over applies to individual families whose breeding seasons differ from the general pattern. Thus the hummingbirds breed mainly from June to December, *Coereba* from April to December, the tanagers from September to February, and the seed-eaters mainly in the first six-months of the year. It seems almost certain that the main season of moult must be in the months March-July.

British Guiana. Lying at the point where the north-tropical and south-tropical dry seasons are equally balanced, the breeding seasons in British Guiana must be of particular interest. It is therefore unfortunate that, as Davis (1954) points out, his own records differ considerably from Beebe's from essentially the same area. Since Davis's records are based on a longer period of continuous residence, and (like the rest of those used in the present paper) do not include gonad records, which constitute an unknown number of Beebe's records, we have used only Davis's data. These show a considerable amount of breeding in all months, with two peaks, a large one in March and April and a smaller one in September (Text-fig. 11d), the former coinciding with the end of the short dry season and the latter with the beginning of the long dry season. It appears that, although climatically the south-tropical dry season is somewhat better developed than the north-tropical dry season, the general breeding season approximates more closely to the northern type. It would be extremely interesting to have quantitative information on moult in this area. One would especially like to know whether, as would be expected, different individuals of the same species are found moulting at two different times of year, and if so, whether some individuals consistently follow a "northern" and some a "southern" annual cycle.

The data are insufficient to allow analysis of the breeding seasons of many individual families, but the following points may be mentioned. The hummingbirds breed mainly from June to November, at the same time of year as at Belem. Thus the main part of their breeding season coincides with the long dry season, when flowers are most abundant (Davis, 1954). The flycatchers show two distinct peaks coincident with the two general peaks of breeding; though the second peak, in August-October, is of shorter duration than the main January-May peak, the number of species found breeding in the two periods was almost the same. The nightjars, which in Trinidad show a single peak in March-May, breed in both the peak periods in British Guiana, though probably less during the second period than the first.

Surinam. Haverschmidt's data are a valuable supplement to the British Guiana records, as they are much more complete for the few species with which they deal (Haverschmidt, 1950, 1952a, 1952b, 1953, 1954, 1955, 1959). They suggest that very long or continuous breeding seasons are rather common (five out of the seven species: *Columbigallina talpacoti, Tapera naevia, Amazilia fimbriata, Troglodytes musculus, Thraupis virens).* The seasonal distribution of the nests of *A. fimbriata* is closer to that of hummingbirds in Trinidad than at Belem (contrary to Davis's records); the breeding season of *T. leucomelas* is also closer to the Trinidad season for *Turdus* species; but *Chelidoptera tenebrosa,* a member of a family that does not occur in Trinidad, breeds mainly in the second half of the year, and thus follows the Belem breeding season more closely. Data are available for too few species to allow a general discussion, but these records illustrate the transitional nature of the breeding season in the neighborhood of the climatic Equator.

More complete information from the above areas and from other critical areas, associated with moult data, would be necessary before a firm conclusion can be reached, but the data summarized above suggest the following tentative conclusions. At Belem, where day-length is practically constant, there is a well-marked breeding season which is clearly related to the rainfall regime in the same sort of way as are the breeding seasons in Trinidad, Venezuela and Central America. Thus the rainfall regime and the associated environmental changes appear to be adequate to exert effective proximate and ultimate control.

In British Guiana, the breeding season again appears to be related primarily to the rainfall regime, here a double one, but the evidence suggests that though the south-tropical (August-November) dry season is more marked than the north-tropical (February-April) dry season, the pattern of the breeding season has a distinctly more "northern" character. If more complete data confirm that this is so, it might suggest that increasing day-length still exerts a proximate effect even at 7° north. However, the difficulties of attributing an important role to day-length in tropical areas where the breeding seasons of different species are very diverse, and mostly rather long, have already been stressed with respect to Trinidad.

A comparison between the data from Trinidad and Costa Rica (Valley of El General) strongly suggests that the breeding seasons in these two areas cannot be satisfactorily explained without reference to the wider regions of which they form a part. The two areas are at approximately the same latitude, both have heavy rainfalls with the dry season at the same time of year, and they have in common many species of birds or closely related pairs of species. Yet while the Trinidad species begin to breed in all months from October onwards to April or May, their Costa Rica counterparts nearly all begin in March or April (a difference which incidentally further reduces the likelihood that day-length is an important proximate factor). Skutch's area, as already mentioned, is a humid enclave surrounded by country subject to a drier, more seasonal climate. It may well be that essentially the same breeding seasons prevail over the more extensive surrounding areas and so are not perfectly adapted to the valley of El General. Likewise, Trinidad's position, only a short distance north of the Guianas, with two nearly equalled balanced dry seasons and two wet seasons, may have resulted in a breeding season more akin to those areas than Trinidad's climate alone would warrant. Skutch's account of seasonal changes in the flora of his area suggests that the whole biotic complex may be more strongly seasonal than in Trinidad. The possibility must not be overlooked that natural selection has led to complexes of closely knit seasonal changes, affecting both animal and plant life, which may prevail over large areas and be adapted to the general climatic conditions of the region but not perfectly adapted to special local conditions.

Skutch's data make it unlikely that the October peak of breeding in Trinidad has any geographical continuity with the autumn recrudescence of sexual activity in resident northern birds. If this were so, some indication of autumn breeding would be expected in Costa Rica. Instead, as suggested above, it is more likely that the October peak in Trinidad is homologous with the September peak in British Guiana, and thus represents the remnant of the main south-tropical peak of breeding.

Summary

An account is given of the annual cycles of Trinidad land-birds based on 4½ years' field work.

The climate of the central part of the Northern Range of Trinidad, where most observations were made, is humid, precipitation averaging nearly 100 inches per year. There is a single dry season, from January to May. The natural vegetation is forest. Systematic observations on the flora showed that there is much flowering throughout the year, with ill-defined peaks in April and November, while the abundance of fruits showed a marked peak in April-June and a minor peak in November. Insect life appears to be most abundant at the beginning of the wet season.

The breeding and moulting seasons are described for each family. There is good evidence in several cases that differences in breeding season are related to the availability of food. In species with long breeding seasons, there is a strong tendency for the intensity of breeding to be bimodal, with a minor peak in October or November (following the moult), and a main peak in April-June.

The breeding season varies locally in Trinidad, being longest in the wettest areas in the east and probably shortest in the very dry areas in the northwest of the island. The same species of hummingbirds begin breeding earlier in open country than in forest, but no other marked differences in breeding season according to habitat were noted.

In the five seasons of observation, no difference was found in the breeding seasons of some species, while in others annual differences of up to five months were noted.

The number of broods per year and intervals between successive broods were determined for several species. In general, 2-4 nesting attempts per year are usual. Intervals between broods vary according to species; in species with long breeding seasons they tend to be short at the peak of the breeding season (usually around May) and long in the dry season.

The moult occurs mainly from July to November, with little annual variation. The rate of moult and total duration of the moult were ascertained for several species.

The ultimate and proximate factors controlling the breeding season are discussed. Food supply is considered to be the main ultimate factor determining at what season each species breeds. Proximate factors are much more obscure, but for some species, at certain times, rainfall is most important. Reasons are given for supposing that changes in day-length cannot be of general importance.

The relative constancy of the season of moult, and variability of the breeding season, both within species and between different species, as well as other considerations, suggest that the long-term control of the whole annual cycle may depend on environmental factors initiating the moult rather than on factors initiating breeding.

A comparison is made between the breeding seasons in Trinidad and other parts of the neotropical region. The survey emphasizes the importance of the rainfall regime and associated environmental changes in both the ultimate and proximate control of breeding seasons. It is suggested that in limited areas breeding seasons may not be perfectly adapted to local conditions, but rather to the climate and associated seasonal changes prevailing over the wider region of which they form a part.

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APPENDIX

Breeding and Moult Records of Trinidad Land-birds

The following table presents a summary of breeding and moulting data for those species for which records were obtained in the course of the present study. A number of published breeding records are also included which satisfy the requirements given on page 3; the sources of all these are listed at the end of the Appendix.

The figures show the numbers of nests in which the first egg was known or calculated to have been laid in the month indicated. All months in which individuals undergoing wing-moult were trapped are indicated by a dash, either by itself or below the figure if nests were also recorded in the same month.

Species	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Crypturellus soui		1	1	1		1	1	1	1	1	1	
Columbigallina passerina		1				1	1 —	1				
Columbigallina talpacoti	7 —	11 —	14	6	4 —	8 —	17 —	18 —	22 —	4 —	9 —	8 —
Columbigallina minuta			1	2	2	1		2	2			
Leptotila verreauxi	2	3	9	8	6	1	5	—	2	4	5	
Leptotila rufaxilla	1	2	4	4	2	5 —	4 —	1 —	—		1	1 —
Geotrygon montana		1		1	3		1					
Touit batavica	1	3										
Tapera naevia			1		1	4	1	1	3	2		
Piaya cayana	1				1		2				1	
Crotophaga ani	1	8	3 —	4	7	6 —	7 —	5 —	12	8	4 —	1
Otus choliba		1	4	2	2							
Glaucidium brasilianum		1	1	1	2		1					
Steatornis caripensis	12	8 —	20 —	10 —	11 —	2	3	3 —	1	—		9
Nyctibius griseus			2	3			1					
Nyctidromus albicollis					2							
Other nightjars	1	1	3	5	1			1				
Chaetura cinereiventris					1	—		—		—	—	
Chaetura spinicauda						1		—				
Chaetura brachyura				3	30	22	18	11 —	4 —			
Cypseloides rutilus		—		1	6	8	8	9	—			
Panyptila cayennensis			1		1							
Glaucis hirsuta	38	69	46	75	71	58	28	1 —	—	—	—	6
Phaethornis guy	4	5	4	5	3 —	4 —	2 —		—	—	1	2
Phaethornis longuemareus	4	5	2			1	—		—			1
Anthracothorax nigricollis	4	3	4	5	5	2			—		—	
Chrysolampis mosquitus	5	6	5	4	9			1				1
Chlorestes notatus					2	2	—	—	—		—	—
Amazilia chionopectus	2	1	3	1			—	—	—		—	1
Amazilia tobaci	7	7	10	4	5 —	3 —	3 —	1 —	—		1	3
Trogon viridis							1					
Trogon collaris			1									
Trogon violaceus		1	1		1		—				1	
Momotus momota				4	3	—	—			—		
Galbula ruficauda		2	7	7		1 —						
Piculus rubiginosus			1	1	4			—	—			
Celeus elegans				1	3		—	—	—		—	
Veniliornis kirkii	1	1							—			1
Xiphorhynchus guttatus			1			2 —	2 —	—	—			
Dendrocincla fuliginosa					2	4 —	1	1 —	1 —		—	—
Synallaxis albescens	2			1	1	2	3	1	5			2
Synallaxis cinnamomea		1			1				1		3	1

BREEDING AND MOULT RECORDS OF TRINIDAD LAND-BIRDS *(continued)*

Species	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Certhiaxis cinnamomea		—				3	2	1	1	2	—	
Sclerurus albigularis	3	2								1	2	5
Sakesphorus canadensis					2		2				—	
Thamnophilus doliatus	3	3	—	1	2	3	2	—	2	1	1	1
Myrmotherula axillaris					—	2	1	1	—			
Formicivora grisea							1	1				
Myrmeciza longipes									1			1
Formicarius analis			2						1			
Pachyrhamphus polychopterus			1	1		1	1		1			
Tityra cayana		1	1								1	
Procnias averano				1	2		1	1		1	1	
Pipra erythrocephala	1		2			4	5	1	—	—	—	—
Manacus manacus	9	23	19	27	46	69	37	35	6	—	—	1
Fluvicola pica	—					3	1	3	1	1	—	—
Arundinicola leucocephala			1				1	3	2	1		
Tyrannus melancholicus	1	2	3	7	6	4	7	3				
Legatus leucophaius		1	2	1	3	3						
Myiodynastes maculatus			1			2						
Megarynchus pitangua		1	1	4	5	2						
Pitangus sulphuratus	3	4	2	7	7	3	1	2		1	1	2
Contopus cinereus			2		3	1	3		—			
Empidonax euleri						1		—		—		
Myiophobus fasciatus			—	1	1		3	3		—	1	—
Platyrinchus mystaceus					1							
Tolmomyias sulphurescens				1		3	2					
Tolmomyias flaviventris							1	1	1			
Elaenia flavogaster		1	1	13	14	7	1	—		—	1	1
Myiopagis gaimardii		1										
Camptostoma obsoletum				1	—		1			1	1	
Leptopogon superciliaris	—		1		4	1	1	—				—
Pipromorpha oleaginea			2	7	18	22	9	2	1	—		
Progne chalybea				1	7	4	2					
Stelgidopteryx ruficollis				1	3			—				
Thryothorus rutilus	4	1	2	4		3	3	—				
Troglodytes musculus	5	5	2	8	11	10	5	4	7	13	7	8
Mimus gilvus	8	9	10	8	13	5	2		4	4	1	
Turdus albicollis	1	6	10	9	11	20	3	3			7	4
Turdus nudigenis				2	52	53	33	11	—	—	—	
Turdus fumigatus	8	19	18	23	26	36	19	1	—	2	18	11
Platycichla flavipes			1	1	1	1						
Ramphocaenus melanurus		1		1		1		3				—
Cyclarhis gujanensis						1	3	—	1	—	1	
Vireo olivaceus				1	1	3		—				
Hylophilus aurantiifrons							2		—	1		
Chlorophanes spiza		—		—	1	1	1		—			
Cyanerpes cyaneus			1			1	1					
Cyanerpes caeruleus				2		1		—	—	—	—	
Dacnis cayana			2			2	2	—	—			
Coereba flaveola	23	7	15	9	6	2	—	1	—	—	1	2

BREEDING AND MOULT RECORDS OF TRINIDAD LAND-BIRDS *(continued)*

Species	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Conirostrum bicolor			1			1						
Geothlypis aequinoctialis		1			1			1		1		
Basileuterus culicivorus			1	1	2	1						
Psarocolius decumanus	+	+	+	+	+							
Cacicus cela	9	21		11	6							1
Psomocolax oryzivorus	2	3			1							
Molothrus bonariensis					2	1	—	2	1	1		
Quiscalus lugubris	1	1			3	10	10	2			1	3
Icterus chrysocephalus		1										
Icterus nigrogularis	1		1	4	4	4	1	1				
Agelaius icterocephalus	—					1	1		3	5	3	
Tanagra trinitatis			2									
Tanagra violacea	1		1	2	5	5	5	1				
Tangara chrysophrys	2			—		1		—				
Tangara mexicana				2	1	2	2	1	—	1		
Tangara gyrola	1		1	1	—	—	3	1	—			
Thraupis virens	8	4	10	31	21	20	11	1		3	1	1
Thraupis palmarum	3	4	21	20	15	25	16	12	1	3	1	1
Ramphocelus carbo	33	14	14	19	20	35	14	9	1	—	—	3
Piranga flava							1			1		
Habia rubica		1	1		3	11	3	2	—	1		
Tachyphonus rufus		1	1	2	6	7	2	1	—	—	1	
Tachyphonus luctuosus				1	1				—	—	—	
Saltator caerulescens	—		2	4	10	3	5	1	1	—	—	—
Tiaris fuliginosa	1				1	—		1	1	2	2	2
Sporophila intermedia	—					3	1	4	1		—	—
Sporophila nigricollis							3				2	
Sporophila lineola						1	5	6				
Sporophila minuta		—			1	2	4	—				1
Oryzoborus angolensis						1			1			
Volatinia jacarina	4	—			2	7	10	8	1	—	1	1
Sicalis flaveola									1			

Sources of Records, Other Than Those Obtained in This Study

(The following abbreviations have been used for authors: B. & S., for Belcher & Smooker (1934-37); J. & M., for Junge & Mees (1958).)

C. soui Williams (1922), Oct.
C. passerina: Williams (1922), Feb., Aug.
L. verreauxi: J. & M., Nov. (1).
L. rufaxilla: Chapman (1894), Feb. (1); Roberts (1934), Aug. (1).
G. montana: B. & S., May (3).
T. batavica: B. & S., Feb. (2).
P. cayana: B. & S., July (2).
T. naevia: Roberts (1934), Aug.; B. & S., June (1).
C. ani: Williams (1922), Feb., July, Aug., Sep. (1 each).
O. choliba: B. & S., Mar. (1), Apr. (1); Chenery (1956), May (1).
G. brasilianum: Williams (1922), May (1); B. & S., Feb., Mar., May (1), July.
N. griseus: Muir (1925), Mar. (1), Apr. (1); B. & S., Mar., Apr., July (1 each).
N. albicollis: Williams (1922), May (1).
P. cayennensis: B. & S., Mar.
P. guy: Williams (1922), Dec. (1); J. & M., Jan. (1).
P. longuemareus: Williams (1922), Jan. (3), Dec. (1); B. & S., Mar. (1).
C. mosquitus: J. & M., Dec.
A. chionopectus: Chapman (1894), Mar. (1); B. & S., Mar. (1).
T. viridis: B. & S., July.
M. momota: B. & S., Apr. (1), May (1).
P. rubiginosus: B. & S., May (2).

C. elegans: B. & S., May (2).
V. kirkii: B. & S., Feb.
X. guttatus: B. & S., Mar., June (1).
D. fuliginosa: B. & S., June (2).
S. albescens: Williams (1922), Jan. (1), June (2), Aug., Sep. (4); B. & S., July (2), Dec. (1).
S. cinnamomea: B. & S., Sep., Nov. (1); J. & M., Nov. (1), Dec.
S. cinnamomea: Roberts (1934), Aug.
S. albigularis: B. & S., Oct.; J. & M., Jan. (3), Nov. (1), Dec. (3).
S. canadensis: B. & S., May (1), July (2).
T. doliatus: B. & S., Jan. (1), Feb. (1), June (2), July (1), Dec.
M. axillaris: B. & S., June (1).
F. grisea: B. & S., June.
F. analis: B. & S., Mar. (1); J. & M., Sep.
P. polychopterus: B. & S., Apr., June, July, Sep.
P. averano: Beebe (1954), May (1).
P. erythrocephala: B. & S., Jan., Mar. (1).
F. pica: Williams (1922), June (2), Aug. (3), Sep., Oct.
A. leucocephala: Williams (1922), July, Aug. (1), Sep. (1); Roberts (1934), Aug. (1).
T. melancholicus: Williams (1922), June (1); J. & M., July (1). Aug. (1).
P. leucophaius: B. & S., Apr. (1).
M. maculatus: B. & S., June (2).
M. pitangua: B. & S., Mar., May (2); Street (1946), May (1).
P. sulphuratus: Williams (1922), Apr. (1), June (1).
C. cinereus: Street (1946), May (1).
M. fasciatus: J. & M., July (3), Aug. (3), Nov.
C. obsoletum: Roberts (1934), July.
P. chalybea: B. & S., Apr., May (1).
T. musculus: Williams (1922), Aug. (1), Sep. (1), Nov. (2), Dec. (1); Roberts (1934), June (1); J. & M., Oct. (1).
P. flavipes: B. & S., Apr., May, June.
R. melanurus: B. & S., Apr.; J. & M., Aug. (1).
H. aurantiifrons: Roberts (1934), July (1).
C. flaveola: Williams (1922), Nov., Dec. (1).
G. aequinoctialis: B. & S., May, Aug., Oct.
B. culicivorus: Cherrie (1908), Mar.
P. oryzivorus: B. & S., Jan. (1), Feb. (2).
M. bonariensis: B. & S., Sep.
Q. lugubris: Williams (1922), June (1), Aug. (1).
I. nigrogularis: Williams (1922), May (1), June (1), July, Aug.
A. icterocephalus: Williams (1922), July.
T. trinitatis: B. & S., Mar. (1).
T. mexicana: B. & S., May.
T. palmarum: Williams (1922), June, July, Aug., Sep., Dec. (1 each).
T. rufus: Cherrie (1908), Mar.; Williams (1922), June (2).
T. luctuosus: B. & S., Apr., May.
T. fuliginosa: B. & S., Jan., May, Aug., Sep., Oct. (2), Nov. (2), Dec. (2).
S. intermedia: Williams (1922), Aug. (4).
S. minuta: Williams (1922), July (2).
O. angolensis: Williams (1922), Sep.
V. jacarina: Williams (1922), Aug. (2), Nov.